CAMBRIAN ELEUTHEROZOAN ECHINODERMS AND THE EARLY DIVERSIFICATION OF EDRIOASTEROIDS

by ANDREW B. SMITH

ABSTRACT. The five genera and thirteen named species of edrioasteroid from the Cambrian are reviewed and, where necessary, redescribed. All are interpreted as sessile suspension feeders, with an external system of radial water vessels and tube feet that functioned in opening the cover plate sheets. The relationships of these five genera to one another and to other edrioasteroid groups is analysed and a revised classification of the Edrioasteroidea is proposed. *Stromatocystites* has fewest autapomorphic characters and is placed as primitive sister group to the other four genera. These fall into two distinct groups: *Totiglobus* and *Walcottidiscus* are rather globular with a reduced dorsal surface, while *Cambraster* and *Edriodiscus* are discoidal with a prominent marginal frame. Three orders are recognized within the Edrioasteroidea: the Edrioasterida, which includes *Totiglobus*, *Walcottidiscus*, and the family Edrioasteridae; the Cyathocystida, for the families Cyathocystidae and Pyrgocystidae; and the Isorophida, which is expanded to include *Cambraster*, *Edriodiscus*, and the families Cyclocystoididae and Agelacrinitidae.

IN the Cambrian there are a small number of echinoderms that have conventionally been classified as edrioasteroids, of which the best known is *Stromatocystites*. Although Pompeckj first described *S. pentangularis* from the Middle Cambrian of Czechoslovakia in 1896, these animals have remained relatively poorly understood. Yet *Stromatocystites* has held an important place in theories of echinoderm phylogeny. Bather (1900, 1915) considered *Stromatocystites* to be ancestral to all eleutherozoan groups and an intermediate between asteroids, echinoids, and holothuroids on the one hand, and cystoids on the other. This view fell largely out of favour when Fell (1962, 1963) proposed that eleutherozoan groups were polyphyletic in origin, and in the *Treatise on Invertebrate Paleontology* (Regnéll 1966) *Stromatocystites* is treated as no more than a primitive edrioasteroid. More recently, however, the phylogenetic status of *Stromatocystites* has been reassessed by both Termier and Termier (1969, 1980), who provided a highly novel interpretation, and myself (Smith 1984a, b; Paul and Smith 1984) where a return to the more traditional view is argued for.

Four other genera of edrioasteroid in addition to *Stromatocystites* have been described from the Cambrian: *Cambraster*, *Walcottidiscus*, *Totiglobus*, and *Edriodiscus*. Because of the importance of these genera to theories of the early history of eleutherozoan echinoderms, a detailed appraisal of their morphology and relationships seemed long overdue. Some species have been described recently in considerable detail, such as *C. elegans* by Ubaghs (1971), *C. tastudorum* by Jell *et al.* (1985), *T. nimius* by Bell and Sprinkle (1978), and *S. walcotti* by Paul and Smith (1984). Others are, however, still poorly known. This paper therefore sets out to review what is known about the morphology of these animals and to examine their relationships, not only with one another but also with other echinoderm groups. However, a detailed comparison between Cambrian edrioasteroids and primitive starfish such as *Archegonaster* will be dealt with in a subsequent paper and is not considered here.

MORPHOLOGY AND ANATOMY

General organization

Although Cambrian edrioasteroids are variable in their overall shape they all share basically the same body plan. All have a skeletal system that is clearly differentiated into dorsal and ventral surfaces. On
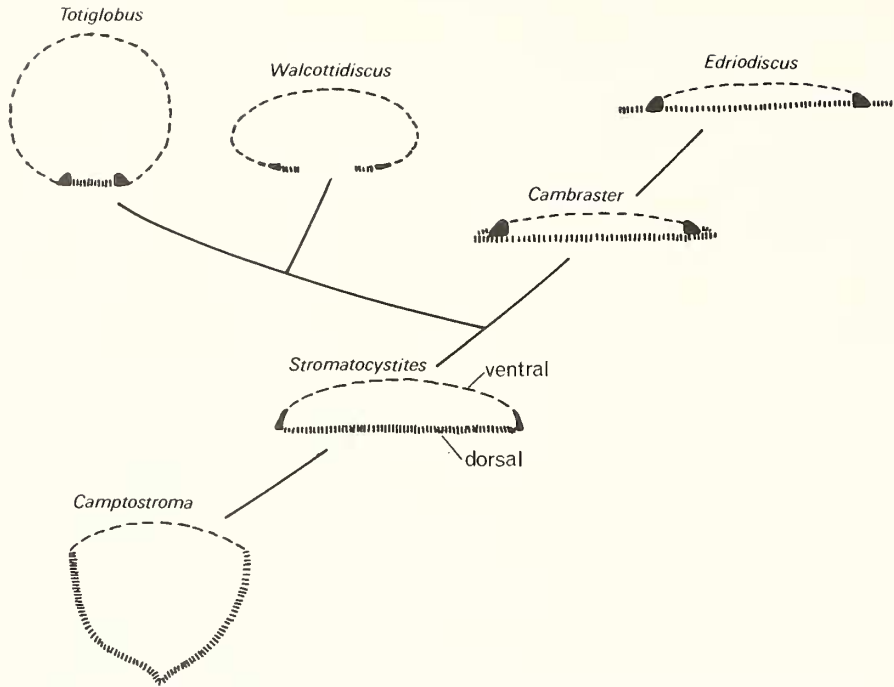
TEXT-FIG. 1. Diagrammatic cross-sections through the five Cambrian genera considered here and *Camptostroma* to show the relative development of dorsal (vertical hatching) and ventral (dashed line) plate surfaces.

the ventral surface there is a central mouth and a marginal anus. Five ambulacral zones radiate from the mouth and are separated by wedge-shaped interambulacral zones. The dorsal surface is composed of a marginal ring of somewhat larger plates surrounding a pavement of flat polygonal plates. In *Stromatocystites* and *Cambraster*, dorsal and ventral surfaces are more or less equally developed so that the boundary between them coincides more or less with the ambitus (text-fig. 1). The two genera differ in that *C. tastudorum* appears to have a double layer of plates outside the marginal ring (Jell *et al.* 1985) which *Stromatocystites* lacks. *Edriodiscus* has a single layer. In *Walcottidiscus* the ventral surface has become enlarged relative to the dorsal surface and the boundary between them now lies sub-ambitally. *Totiglobus* has become even more extreme and its dorsal plating is reduced to a relatively minute disc (text-fig. 1); the ventral surface is expanded and extends well below the ambitus. Thus the relative development of dorsal and ventral surfaces is largely responsible for the differences that exist in overall shape. All are sub-circular to sub-pentagonal in outline but whereas *Stromatocystites*, *Edriodiscus*, and *Cambraster* have a fairly flat profile, *Walcottidiscus* has a depressed ovoid profile and *Totiglobus* is almost globular.

Digestive system

The mouth lies centrally on the ventral surface at the point of convergence of the five ambulacra. It does not open directly to the exterior, but is roofed over by a series of cover plates which may or may not have been able to open in life. The peristomial opening is relatively small and in *S. walcotti*, *Cambraster*, and *Totiglobus* is surrounded by a fixed mouth frame of ambulacral plates. In *S. pentangularis*, however, the mouth may have been more flexible as there is some evidence that the two columns of plates in each ambulacrum were able to separate along the perradial suture

proximally, as in many primitive starfish. Unfortunately, the detailed arrangement of plates in the oral area of this species is still unknown.

The anus also opens through the ventral surface and is situated marginally in the C/D interambulacrum. In *Stromatocystites* and *Cambraster* the periproct is a moderately large circular zone of lath-like plates arranged radially (text-figs. 2 and 7). A similar periproctal system, but with fewer and more organized plates, is present in *Totiglobus*. The periproctal plates lie either flush with the surrounding interambulacral plates or are slightly raised to form a low conical mound.

Since both mouth and anus lie on the same surface, the digestive system must, at the very least, have been looped. The ubiquity of torsion in the digestive tract of all echinoderms, both larval and adult, suggests that the digestive tract in edrioasteroids was also coiled. Bather (1915) argued that the gut probably coiled anticlockwise in edrioasteroids because of a certain asymmetry in the arrangement of periproctal plates. No such asymmetry can be detected in the Cambrian species and the direction of coiling must remain uncertain. However, an anticlockwise coiling seems the most likely since the hydropore/gonopore opens close to the peristome on the right-hand side of the C/D interambulacrum, and such a direction of coiling of the digestive tract would leave more room for the internal gonad in this position. By inference from living groups the digestive system presumably consisted of a short oesophagus descending from the mouth, leading to a coiled intestine and then to a short rectum.

Dorsal surface

Plates of the dorsal surface can be divided into two groups: those that form the marginal ring and those that form the remainder of the dorsal surface. In *Stromatocystites* plates of the marginal ring are poorly differentiated from the other dorsal plates and lie supra-ambitally. They are moderately large, weakly geniculate plates with a rounded adoral edge and flatter, broader adapical edge which faces the substratum. There are no sutural epispires along any of the plate margins; although adjacent plates abut, their zone of contact is narrow and they would not have been able to form a rigid marginal frame. Internally these marginal plates are gently concave and lack internal processes or other evidence of muscle attachment areas. Marginal plates in *Cambraster* are greatly enlarged and form a prominent frame to the ventral surface (text-fig. 2). There are eighteen to twenty marginal ossicles in the ring. These ossicles are triangular in cross-section and adjacent ossicles firmly abut. Their lateral faces are smooth, without crenulation, so presumably the ossicles were bound together by collagenous ligament to form a fairly inflexible marginal frame. Ossicles at each radius have a V-shaped notch where the ambulacral flooring plates extend on to the marginal frame (text-fig. 2). *Totiglobus* also possesses a stout marginal ring of abutting ossicles; this ring would have been rather poorly flexible. Marginal ossicles are hardly distinguishable from the exterior but have large internal processes (see Bell and Sprinkle 1978, text-fig. 4) which presumably were associated with muscle attachment. As the processes face towards the centre of the dorsal surface, these could well have been attachment sites for radially arranged dorsal muscle fibres necessary if the dorsal surface acted as a suction pad. Details of the marginal plates in *Walcottidiscus* are poorly known. Externally the marginal plates are not clearly differentiated and, as in *Totiglobus*, there is no recognizable tesselate ring of plates. Whether the marginal ring plates were more clearly differentiated internally is unknown.

There is an irregular pavement of tesselate, polygonal plates within the marginal ring. The entire dorsal surface is plated in all but *Walcottidiscus* where there is a central uncalcified zone. All of the dorsal plates in *Stromatocystites* are similar in thickness. There is a large equant plate at the centre of the dorsal surface which is surrounded by a variable number of large, radially elongate plates (text-fig. 4). Dorsal plates decrease in size away from the centre of the disc and, immediately adjacent to the marginal ring, there is a zone of tiny lath-like platelets that may not fully abut. This is the region of plate addition where new dorsal plates were added immediately inside the marginal ring. It is also a region of high flexibility. Dorsal plating in *Totiglobus* is very like that in *Stromatocystites* except that there is no clearly distinguishable central plate. Only a small number of polygonal plates lie within the marginal ring and these are smooth externally but weakly ridged and grooved internally (see Bell and
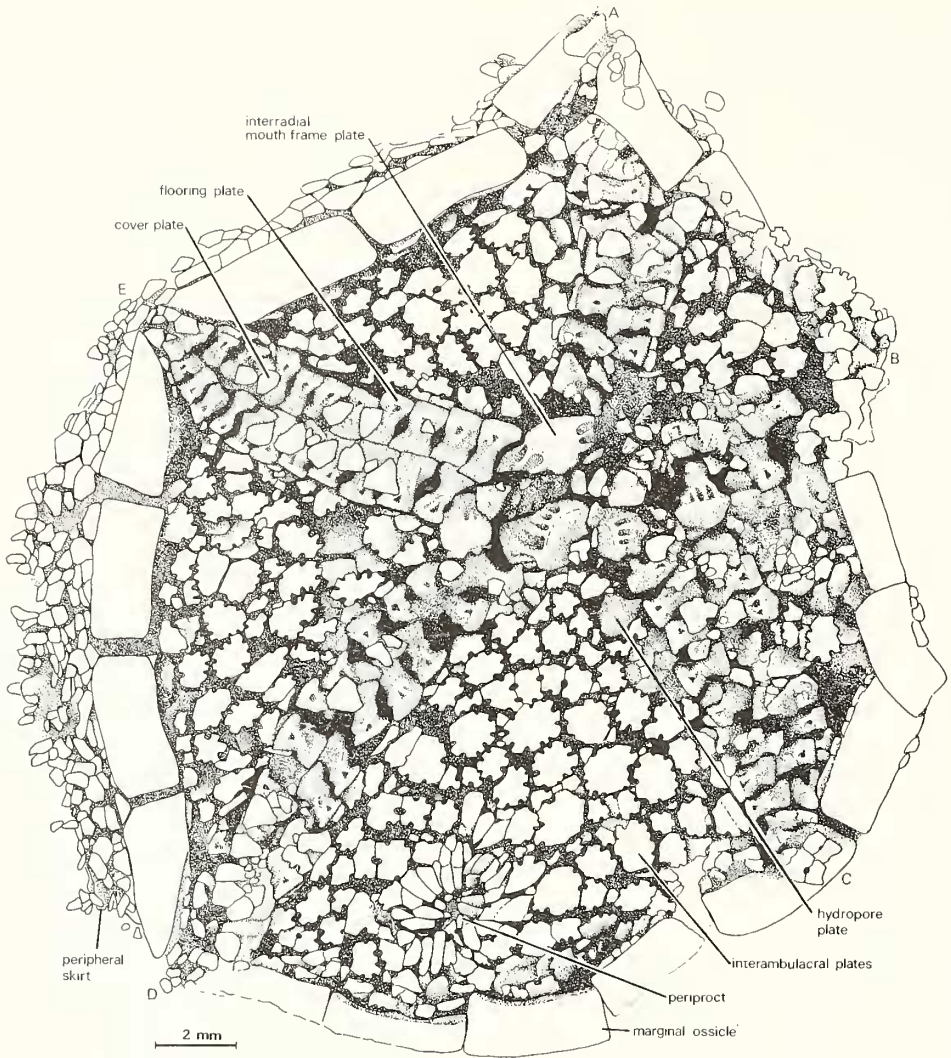
TEXT-FIG. 2. *Cambraster cannati* (Miquel, 1894), camera lucida drawing, ventral surface of holotype of *C. elegans* Termier and Termier, 1969, from a latex, BM(NH) E63135 (see text-fig. 19A). Original is in the collections of the Museum of le Havre, France.

Sprinkle 1978, text-fig. 4*b*). All plates are tessellate and plate size decreases quite noticeably towards the outer edge.

Cambraster has a central zone of small polygonal plates surrounded by one or two circles of large polygonal plates. Over much of the central region of the aboral surface the plates are relatively thin and sub-tessellate, fitting together to form a continuous pavement. All known specimens of *C. cannati* show rather distorted and jumbled plating but there are two clear circles of large, radially elongate, polygonal plates which either abut or have small plates intercalated in between (text-fig. 2). There is only one circle of plates in *C. tastudorum*, all of which are contiguous (Jell *et al.* 1985). Plates become thicker and more obviously polygonal towards the margin, but at the very distal edge there are small lath-like plates which probably extended slightly beyond the marginal ossicles (text-fig. 2; see also
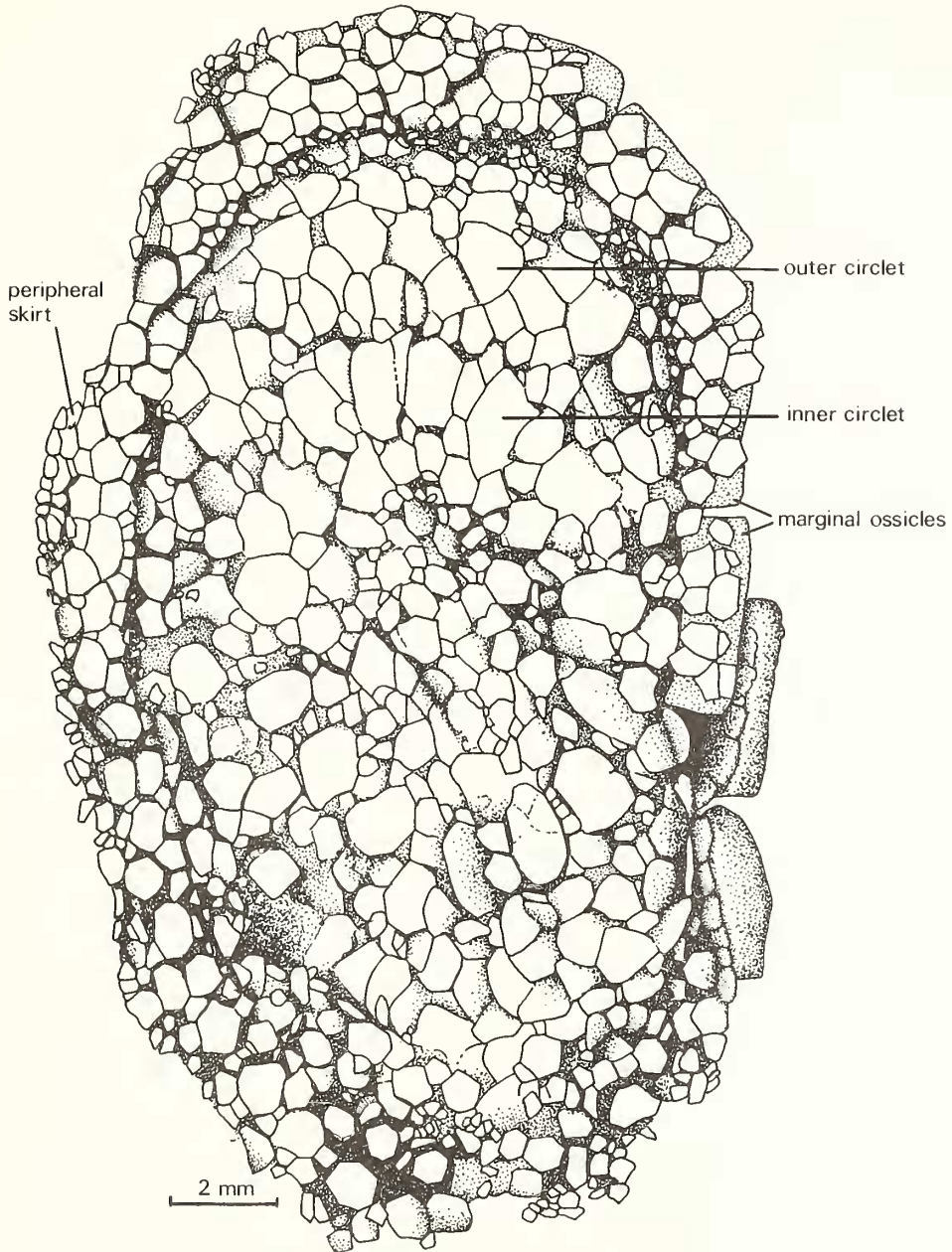
TEXT-FIG. 3. *Cambraster cannati* (Miquel, 1894), camera lucida drawing of dorsal surface of holotype of *Eikosacystis miqueli* Termier and Termier, 1969, from a latex, BM(NH) E63136 (see text-fig. 19c, D). Original is in the collections of the Museum of le Havre, France.
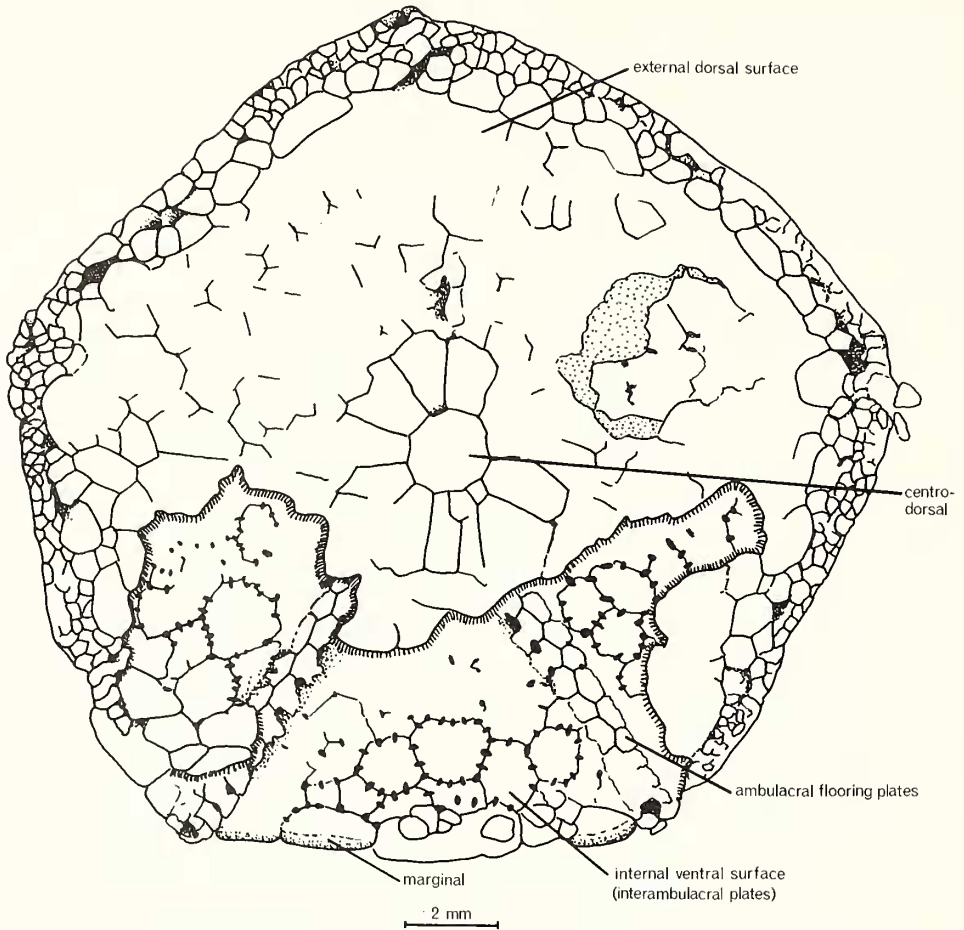
TEXT-FIG. 4. *Stromatocystites walcotti* Schuchert, 1919, USNM 66443, camera lucida drawing of the holotype, showing the dorsal surface and part of the interior of the ventral surface where the dorsal surface has been damaged.

Ubaghs 1971). The dorsal surface is slightly larger than the ventral surface, so that the marginal ossicles lie just above the ambitus and are hidden from sight when viewed from beneath.

Edriodiscus, like *Stromatocystites* and *Cambraster*, is fully plated, but here all the plates within the marginal ring are of very much the same size. These are flat, polygonal, and tesselate. There is a ring of flat-based, cylindrical marginal ossicles which form a frame, as in *Cambraster*. Here, however, the marginal ossicles are inserted into the dorsal surface plating so as to separate a peripheral skirt of smaller plates from the main central pavement (text-fig. 20). All plates are covered with radially arranged ridges and grooves, very reminiscent of the ornamentation on the lower surface of peripheral skirt plates in isorophid edrioasteroids.

The structure of the outer zone of calcite plates in *Walcottidiscus* is not clearly seen. There appears to be a large number of small lath-like plates which, in general appearance, resemble the dorsal plating found in *Edrioaster*.

It is quite clear that neither *Stromatocystites* nor *Cambraster* had any means of attaching to the substratum by their dorsal surfaces, at least as adults, and must simply have lain unattached on the

sea floor. *Walcottidiscus*, on the other hand, had a large uncalcified dorsal pad which presumably acted as some form of adhesion disc. *Edriodiscus* has prominent radially arranged ridges and grooves, like those found on the lower surface of peripheral plates in agelacrinitids. This structure is undoubtedly associated with attachment but the precise function of the ridges remains uncertain. The question remains whether *Totiglobus* had any means of attachment. Bell and Sprinkle (1978) thought that the entire dorsal surface within the marginal ring may have acted as a suction pad. Certainly it is hard to imagine how a globular animal such as *Totiglobus* could have been stable with such a small base unless it was able to attach itself. This might have been achieved through various means, but the large internal processes on the marginal ring ossicles suggest that adhesion was achieved through suction. If the dorsal surface was moderately flexible immediately within the marginal ring, then radially arranged muscles running from the centre of the dorsal surface to these internal processes might have been able to pull the dorsal pad inwards to create suction.

Ventral surface

Interambulacral areas. The interambulacral zones in *Stromatocystites* and *Cambraster* are composed of a large number of polygonal, tesselate plates (text-fig. 13). Epispires are present along the plate sutures except immediately adjacent to ambulacral plates, marginal ossicles, and plates of the periproct. Epispires presumably provided egress for external finger-like extensions of the body coelom that functioned in gaseous exchange and presumably resembled papillae of Recent sea-stars. *Totiglobus*, *Walcottidiscus*, and *Edriodiscus* all lack interambulacral epispires and their plating is tesselate to sub-tesselate. New interambulacral plates were added adjacent to the marginal ring.

Ambulacral zones. The five ambulacra are arranged in a 2:1:2 pattern. Close to the mouth the A and B and the D and E rays combine to make a T-shaped junction with ambulacrum C above the mouth (text-fig. 15). The ambulacra in *Cambraster* and *Stromatocystites* are straight and continue right to the edge of the ventral surface. The tips of the ambulacra are actually inserted between the ossicles of the marginal ring in both genera and could therefore grow only at the same rate as the body as a whole. *Edriodiscus* has weakly curved ambulacra which still reach the marginal ring. *Totiglobus* has straight ambulacra but, although these extend below the ambitus, they do not reach the marginal ring. The ambulacra in *Walcottidiscus* extend to the ambitus and then curve sinistrally. Ambulacra are initially straight in juveniles but curve to grow around the body in adults. Ambulacra form the animals' food-gathering surfaces, so their length relative to body size is obviously crucial. *Totiglobus* and *Walcottidiscus* arrived at different solutions to the problem of how to increase their food-gathering surface relative to general body size. *Totiglobus* increased its ambulacra by expanding the entire ventral surface relative to the dorsal surface, whereas *Walcottidiscus* evolved curved ambulacra so that their growth was not constrained by the marginal ring but could continue around the periphery.

The detailed structure of the ambulacra is very similar in all genera. Each ambulacrum consists of a biserial column of flooring plates which are roofed over by two multiplated series of cover plates. The morphology of the flooring plates is known in detail only for *Stromatocystites*, *Cambraster*, and *Totiglobus*. Similar flooring plates are probably present in *Walcottidiscus* but here only the narrow external face of the flooring plates can be seen. Individual flooring plates are rather squat, particularly in *Stromatocystites*. There is a small rectangular abradial face which is exposed externally between the interambulacral plates and the cover plates (text-figs. 6 and 8c). This is generally smooth and flat, and adjacent faces abut. The rest of the flooring plate lies hidden beneath the cover plate series. Flooring plates are arranged alternately and the two columns meet perradially along a weakly zigzagged suture. This suture becomes almost straight distally in *Cambraster*, but in *Stromatocystites* and *Totiglobus* the ambulacral plates firmly interlock along the mid-line. There is a moderately large sutural pore between successive plates in each column, passing from the interior of the test to the ambulacral channel. The pore is circular to ovoid in outline and is more or less equally shared between the two plates. It occupies the outer half of the adradial face (text-fig. 6) and therefore opens immediately beneath the cover plates. On the upper face, this pore is sometimes surrounded by a slight rim. In the central region between sutural pores the flooring plate is expanded into a broad
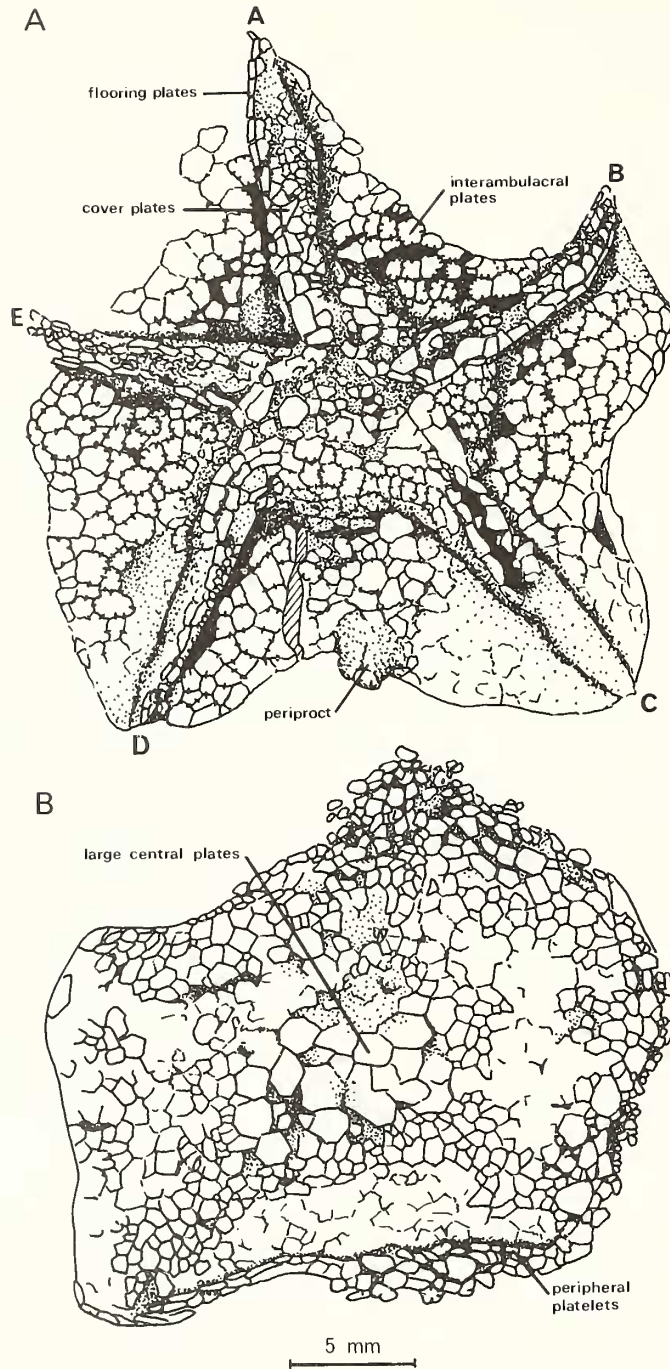
TEXT-FIG. 5. *Stromatocystites pentangularis* Pompeckj, 1896, camera lucida drawings. A, BM(NH) E16004, ventral surface. B, BM(NH) E63138 (latex kindly supplied by Professor G. Ubaghs), dorsal surface of a specimen in the collection of Dr Krantz of Bonn.

V-shaped ridge (text-fig. 6). This ridge has a small but distinct pit situated immediately beneath the cover plates and opening upwards; it is presumably a ligament pit for the collagenous fibres necessary to bind the cover plates to their flooring plates. The perradial portion of the flooring plate is smooth, weakly concave, and forms a shallow channel. The inner face of the flooring plates is unnoteworthy, except in *S. walcotti* where there are paired lateral prongs (text-fig. 7). What the three dimensional shape of these flooring plates is and what purpose the paired prongs served is not at all clear. Where the perradial suture is obviously zigzag, the ambulacral flooring plates must have been more or less rigidly fixed, but in *Cambraster*, where this suture becomes almost linear towards the tips of the arms, it is quite possible that the ambulacra had a certain amount of flexibility and could widen or narrow the ambulacral groove as necessary.
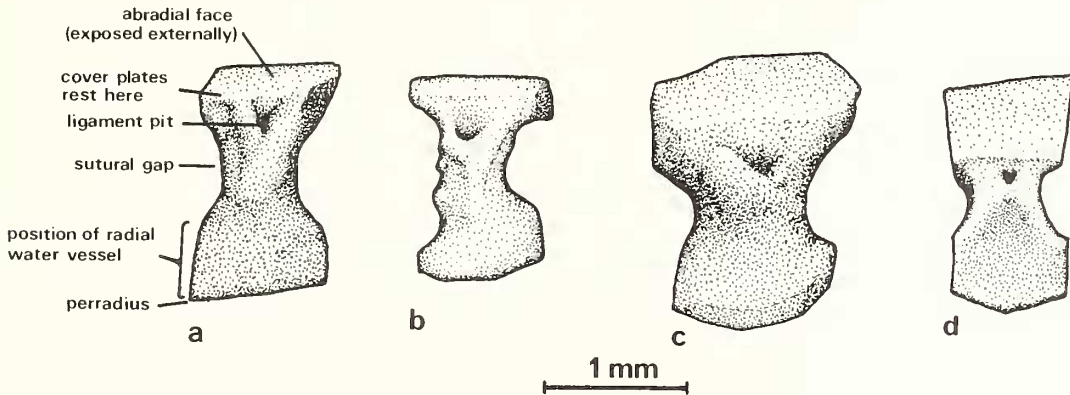

TEXT-FIG. 6. Ambulacral flooring plates, ventral view. *a*, *Cambraster cannati* (Miquel, 1894), detail of one plate from the specimen illustrated in text-fig. 2. *b*, *c*, *Stromatocystites pentangularis* Pompeckj, 1896; *b*, BM(NH) E63099; *c*, BM(NH) E63103. *d*, *Totiglobus nimius* Bell and Sprinkle, 1978, drawn from Bell and Sprinkle (1978, pl. 2, fig. 2).

Cover plates are arranged as a multiple series and attach along the inner border of the flooring plates (text-fig. 14). Distinctly larger primary cover plates are always developed, and towards the distal tip of the ambulacra may be the only cover plates present. Primary cover plates are pentagonal in outline with a broad flat base that rests on the flooring plate, and a distal point. One primary cover plate sits on each flooring plate, except in *Walcottidiscus* where there appear to be two per flooring plate (Pl. 89, fig. 4). Primary cover plates lie either directly above their corresponding flooring plate or slightly offset, as in some specimens of *Totiglobus* (Bell and Sprinkle 1978). There may be smaller plates occasionally inserted between the primary cover plates in *Stromatocystites*, but in other genera the primary cover plates abut each other.

The inner face of each primary cover plate has a distinct ridge that runs slightly obliquely from the proximal edge to the distal point. This becomes less prominent away from the flooring plate and fades. A second, less pronounced ridge can also be made out in some, convergent with the first. This defines a central triangular area on the inner face of the cover plate that possibly marks the position of ligament attachment.

Distal to the primary cover plates comes an irregular array of smaller, secondary cover plates. These are most numerous in *Walcottidiscus*, where there may be four or five irregular rows, whereas in *Stromatocystites* and *Cambraster* they form only a narrow band. In *Totiglobus* there is only a single secondary cover plate inserted between the distal edges of adjacent cover plates. In well-preserved specimens the paired cover plate series meet along the perradius to enclose the ambulacral groove; the perradius often appears slightly sinuous.
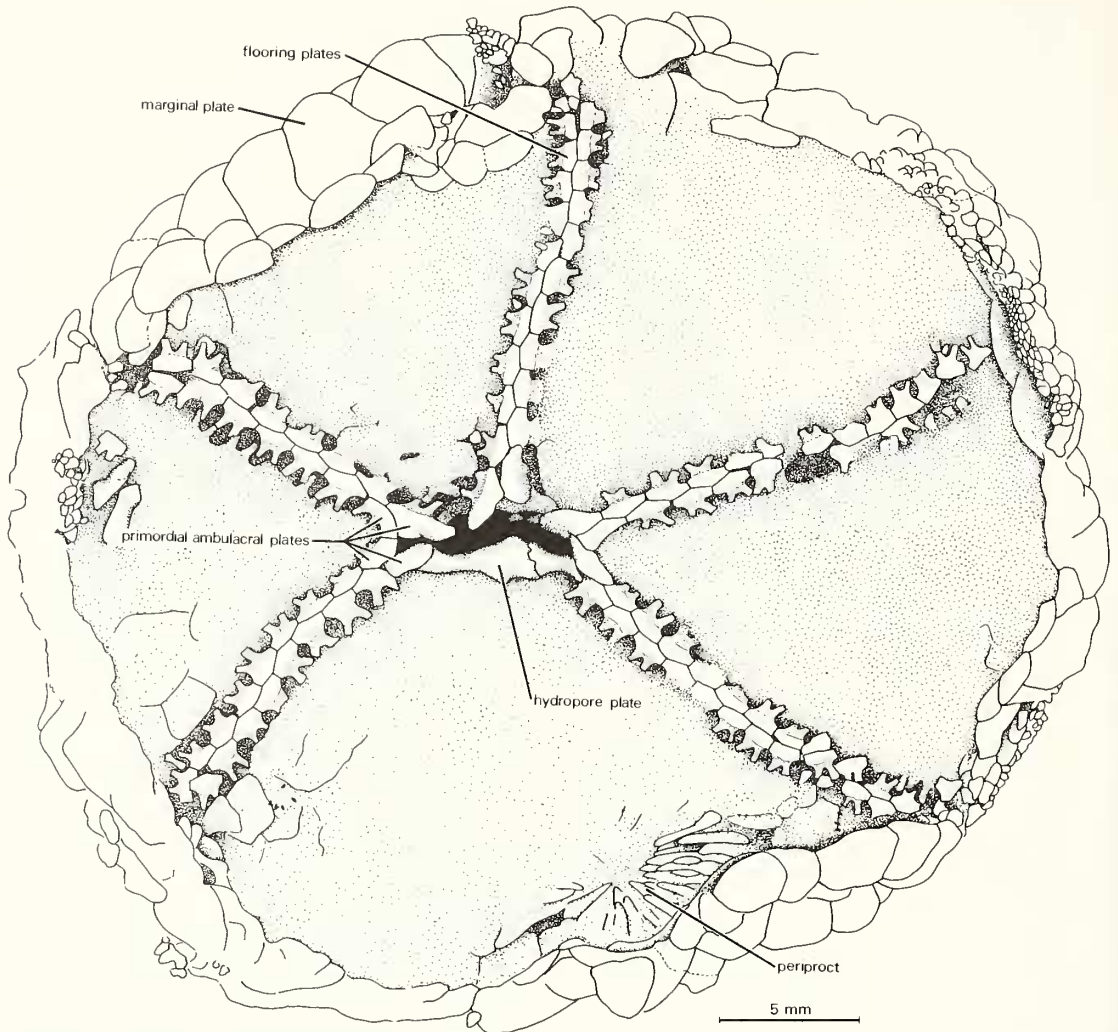
TEXT-FIG. 7. *Stromatocystites walcotti* Schuchert, 1919, USNM 376690, camera lucida drawing, showing the interior of the ventral surface and oral frame structure; no locality data, but the matrix is similar to other specimens of *S. walcotti* from Bonne Bay, Newfoundland.

Oral area. The precise arrangement of plates in the oral area is largely unknown in the majority of species. In all except possibly *S. pentangularis* the most proximal ambulacral flooring plates are firmly bound together to form a fixed oral frame. In *S. walcotti* only the most proximal flooring plate in each column, together with the large elongate hydropore plate, are involved in the oral frame (text-fig. 7). The first flooring plates from adjacent ambulacra meet interradially so as to exclude any inter-ambulacral plates from the peristome margin. The hydropore plate is large and asymmetrical, with a broad inward sloping face on the right hand side. This plate lies in interambulacrum C/D. As yet no external hydropore opening has been observed and the stone canal may have opened directly into the peristomial cavity. Both *Cambraster* and *Totiglobus* have an oral frame that consists of five large interradial elements. These appear to have formed through fusion of the first two ambulacral plates in adjacent ambulacral columns (i.e. they are composed of four plates in total). These plates are very

distinctive, having a broad triangular external face and an adradial face with two ridges and pits on each side (text-fig. 2). The pits may represent passageways that have been lost in fusion. The hydropore in *Totiglobus* opens as a slit-like pore between two plates, one of which is the oral frame element in the C/D interray, the other being the next proximal flooring plate in ambulacrum C or an adjacent interambulacral plate (Bell and Sprinkle 1978, text-fig. 2). In *C. caunati* the oral frame is disrupted in the best preserved specimen and the exact location of the hydropore is uncertain. However, there is a large interambulacral plate lying close to the peristome in the C/D interray which is almost certainly the hydropore plate (text-fig. 2); this was probably in contact with the mouth frame plate of that interray in life. The hydropore is clearly seen in *C. tastudorum* where the opening lies between the C/D ambulacral mouth frame and the hydropore plate (Jell *et al.* 1985). As in many edrioasteroids the arrangement of cover plates in the oral area is undifferentiated from that of the ambulacra and no large plates stand out.
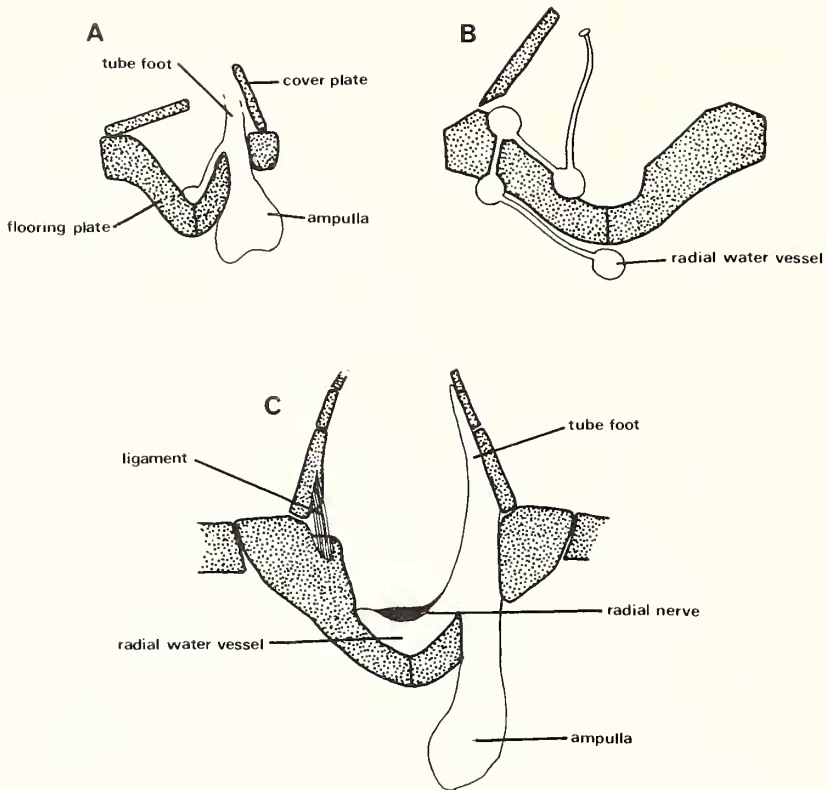
The water vascular system

The presence of radially arranged ambulacra and a hydropore shows that these Cambrian genera possessed a water vascular system, like all other echinoderms. From the single, off-centred hydropore a short stone canal would have descended to the circum-oesophageal ring. There is little direct evidence as to where this ring lay, but the shallow ledge on the adoral face of the mouth frame plates in *Totiglobus* and *Cambraster* may mark its position.

The ambulacra were unquestionably associated with radial water canals that ran from the circum-oesophageal ring to the tip of each ambulacrum. The position of this water vessel has been interpreted in two contrasting ways. Bather (1915), when faced with an almost identical arrangement in *Edrioaster*, thought that the radial water vessel lay above the flooring plates and that the sutural passageways between adjacent flooring plates connected external tube feet to their internal ampullae (text-fig. 8A). This arrangement was also favoured by Paul and Smith (1984) for *Stromatocystites*. Bell (1977), however, argued that edrioasteroids possessed an internal radial water vessel that gave rise to a rather complex arrangement of tubes and bulbs (text-fig. 8B); Bell and Sprinkle (1978) applied this model to *Totiglobus*. Bell produced three arguments in support of his interpretation. First, he noted that in some isorophid edrioasteroids there are pores between adjacent cover plates that lead not into the ambulacral grooves but directly into the thecal interior. These he interpreted as being passageways for tube feet. However, isorophids are a highly derived group with flooring plates that are completely different from those of *Edrioaster* and *Stromatocystites*. Even if Bell is correct in interpreting these cover plate pores as passageways for tube feet, nothing equivalent is found in the Cambrian genera and the arrangement of the water vascular system in the highly derived isorophids is not necessarily the same as in more primitive groups.

Bell's second observation was that in edrioasteroids the hydropore lies on the outer side of the mouth frame, making it rather implausible that the stone canal looped under the mouth frame to reach the externally situated circum-oesophageal ring. He thought it much more likely that the stone canal would simply have descended to an internal ring vessel which then gave rise to internal radial water vessels. Yet this arrangement with external radial water vessels and hydropore situated distal to the mouth elements is precisely what occurs in pelmatozoans, asteroids, and primitive 'ophiuroids'.

Thirdly, Bell suggested that the ambulacral pore lay too close to the cover plates to have allowed the tube feet room to function efficiently, and therefore that the ambulacral pore was for egress of the radial water vessel. This argument collapses if the function of the tube feet in these animals was to open the cover plate skirt, as Paul and Smith (1984) suggested. The tube foot would then need to have been positioned close to the cover plate attachment zone, and possibly even connected to the cover plate sheet. The flooring plate passageways would then have led from the tube feet to their internal ampullae which served as fluid reservoirs and allowed the tube feet to inflate and deflate independently (text-fig. 8C). As embryological studies have shown that an internal radial water vessel is a derived character, and as all pelmatozoans and the more primitive eleutherozoans have external radial water vessels, it seems much more probable that in these Cambrian genera the radial water vessel lay above the flooring plates in the ambulacral tunnel. One of the prime reasons for having

A

tube foot
cover plate

flooring plate
ampulla

B

radial water vessel

C

ligament
tube foot

radial nerve

radial water vessel

ampulla

TEXT-FIG. 8. Diagrammatic cross-sections through ambulacra showing flooring plates, cover plates, and the inferred arrangement of the water vascular system according to: A, Bather (1915); B, Bell (1977); C, this paper.

a series of cover plates above the ambulacral tunnel must surely have been to provide protection for the radial water vessel and associated nerves. The smooth perradial channel on the floor of the flooring plates presumably marks the position of this vessel.

MODE OF LIFE

From the preceding description it would appear that Cambrian edrioasteroids were sessile, low-level suspension feeders. They lived either unattached on the sea floor or fixed to the substratum by their dorsal surface, which in some was modified into a suction pad. All lived with their oral surface facing upwards away from the sea floor. This is suggested by their shape, since they have a flat dorsal surface and a weakly to strongly convex ventral surface, and by the presence of ventral epispires in some genera. Epispires are directly connected with gaseous exchange and no echinoderm has respiratory structures on the lower rather than the upper surface. Food must have been captured by the ambulacra and transported to the mouth along the ambulacral grooves, since these converge upon the mouth. When the animal was feeding the cover plate sheets must have been open to expose the ambulacral grooves. The simplest mechanism for raising the cover plate sheets would have been through inflation of the closely adpressed tube feet. If the prominent pit on the outer face of each cover plate is correctly interpreted as a ligament pit, then connective tissue running from this pit to a corresponding depression on the inner face of primary cover plates could have acted like a tension

spring, pulling the cover plate skirt back down over the ambulacral groove when the tube foot deflated. As both mouth and food gathering surfaces were situated on the upper surface, these animals could not have been detritus feeders but must have eaten fine particulate matter in suspension, like pelmatozoan echinoderms. Presumably they were ciliary mucus feeders, using ciliary currents to draw particulate matter into the ambulacral grooves and mucus to trap this material and pass it to the mouth. Both functions could have been performed by the epithelial lining of the flooring plates and the inner surface of the cover plates, although it is possible that there may have been additional crinoid-like tube feet arising directly from the radial water vessel to assist in food capture.

Termier and Termier (1969) suggested that *Stromatocystites* and *Cambraster* were infaunal, living beneath a thin covering of sediment and drawing water with suspended nutrients into permanently sealed ambulacral grooves through orifices at the tip of each ambulacrum. However, the distal orifices that they described are post-mortem artifacts caused by the collapse of the distalmost cover plates in two ambulacra in the holotype of *S. walcotti*. These animals are also unlikely to have lived infaunally since, unlike the asteroids with which the Termiers drew comparison, they had no paxillae to maintain a water-filled space around their buried body, which would have enabled the papillae to continue functioning.

PHYLOGENETIC ANALYSIS

The evolutionary relationships of Cambrian edrioasteroids are important for the analysis of the early history of eleutherozoan echinoderms. The major eleutherozoan groups, such as the asteroids, echinoids, and holothuroids, do not appear in the fossil record until after the Cambrian; the same is true for a number of important edrioasteroid groups. So, can any of these lineages be traced back into the Cambrian? The relationship of *Stromatocystites* to other Lower Cambrian echinoderms has already been analysed by Paul and Smith (1984) who also briefly sketched the later diversification of eleutherozoans. Here I attempt a more detailed analysis of how the Cambrian edrioasteroids relate to later groups.

For this phylogenetic analysis outgroup comparison has been made with the Lower Cambrian genus *Camptostroma*. The reasons for placing this genus as one of two primitive sister groups of *Stromatocystites* were fully dealt with by Paul and Smith (1984). They considered *Camptostroma* to be intermediate between *Stromatocystites* and the Cambrian pelmatozoans. The characters that seem to be important in determining relationships between the five Cambrian genera are listed in Table 1. Despite our lack of knowledge about certain morphological attributes in some of these genera, a reasonable cladogram can be drawn up (text-fig. 9). All five genera differ from *Camptostroma* in having a flattened dorsal surface, rather than a squatly conical dorsal surface capable of some degree of spiral elongation and contraction. Their body-wall skeleton is also only one layer thick and composed of tessellate plates dorsally, whereas in *Camptostroma* the skeleton is multilayered and dorsal plating is clearly imbricate.

Of the five Cambrian genera, *Stromatocystites* has the fewest novel characters in comparison with *Camptostroma* and other Lower Cambrian echinoderms, and is placed as the primitive sister group to the rest. The remaining four genera fall into two groups of two. *Walcottidiscus* and *Totiglobus* share the synapomorphies of having a rather globular body form (as a result of relative expansion of the ventral surface and reduction of the dorsal surface), the loss of interambulacral epispires, the presence of a basal suction pad, and ambulacra whose distal tips are not inserted into the marginal ring of ossicles. *Cambraster* and *Edriodiscus* are quite different in shape, with an extensive flat dorsal surface and a slightly smaller ventral surface. Their marginal ossicles, which are relatively poorly developed in the other genera, are large and stout with a roughly triangular cross-section; this is taken as a synapomorphy for the group. In both *Cambraster* and *Edriodiscus* the dorsal pavement of plates extends slightly beyond the marginal ring to form a peripheral sheet, although *Edriodiscus* is more advanced in having the marginal ossicles actually inserted into the dorsal pavement. *Totiglobus* and *Cambraster* share two important characters which are not present in *Stromatocystites* but which, by implication, should also be present in *Edriodiscus* and *Walcottidiscus* (although these are too poorly
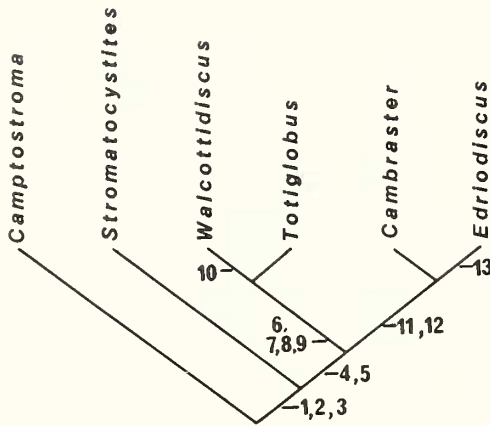
TEXT-FIG. 9. Cladogram of character distribution for the five genera of Cambrian eleutherozoans; characters 1–13 are given in Table 1.

known at present): 1, an identical mouth frame composed of five interradial elements, each of which is formed by fusion of four proximal flooring plates, two from each adjacent ambulacrum; 2, a discrete hydropore plate that lies adjacent to the mouth frame but is not incorporated into it.

Relationships with other groups

Edrioasterids. The Ordovician family Edrioasteridae currently contains just two genera: *Edrioaster* and *Edriophus.* They have the same overall shape and plating arrangement as *Totiglobus* and *Walcottidiscus,* with ambulacra that extend sub-ambitally, a ring of enlarged ossicles around the dorsal surface, and an uncalcified zone at the centre of the dorsal surface. Their mouth frame consists

TABLE 1. Distribution of characters in Cambrian genera of edrioasteroids. *Camptostroma* is taken as being primitive for outgroup comparison.

Derived character state	*Stromatocystites*	*Cambraster*	*Edriodiscus*	*Totiglobus*	*Walcottidiscus*
1. Flat, tesselate dorsal surface	×	×	×	×	×
2. Dorsal plating one layer thick	×	×	×	×	×
3. Marginal ring of plates present	×	×	×	×	×
4. Mouth frame composed of five fused ambulacral flooring plates, interradially positioned	—	×	?	×	?
5. Hydropore plate excluded from oral frame	—	×	?	×	?
6. Interambulacral plates tesselate; no epispires	—	—	?	×	×
7. Dorsal surface acting as suction pad	—	—	—	×	×
8. Dorsal growth reduced relative to ventral growth	—	—	—	×	×
9. Ambulacral tips free of marginal ring	—	—	?	×	×
10. Central region of dorsal surface uncalcified	—	—	—	—	×
11. Marginal ossicles stout, forming a prominent ring	—	×	×	—	—
12. Peripheral skirt extending beyond marginal ossicles	—	×	×	—	—
13. Marginal ossicles inserted into dorsal pavement	—	—	×	—	—

of five interradial elements, each formed through the fusion of proximal flooring plates, but they are unique in also having five radially positioned elements which underlie the flooring plates (see Bell 1976), a feature which can be taken as a synapomorphy for the two genera. The interambulacral zones are identical to those of *Totiglobus* and *Walcottidiscus*; ambulacral zones are similar but possess enlarged primary cover plates and greatly reduced secondary cover plates. Bell and Sprinkle (1978) suggested that *Totiglobus* might be ancestral to edrioasterids. However, *Walcottidiscus* is taken as the primitive sister group here rather than *Totiglobus* since *Walcottidiscus* and edrioasterids share two advanced characters: 1, ambulacra that curve around the ambitus; 2, a central uncalcified zone to the dorsal surface.

Isorophids. The majority of isorophid edrioasteroids have been reviewed recently by Bell (1976) in admirable detail and the group is therefore relatively well understood. Isorophids share the following four advanced characters that distinguish them from other edrioasteroids: 1, uniserial flooring plates lacking sutural passageways; 2, an oral frame composed of the first flooring plate in each ambulacrum; 3, ambulacral cover plates that extend intrathecally and completely conceal the flooring plates; 4, an uncalcified dorsal surface. These are all autapomorphies of the group. Bell (1976) divided isorophids into two suborders and four families, carefully listing the diagnostic features of each. However, he did not distinguish between symplesiomorphic and synapomorphic character states and, in the light of what is now known about the Cambrian edrioasteroids, it is worth examining these groupings cladistically. Table 2 gives an analysis of the characters used by Bell (1976) and identifies those that are apomorphic and can be used in constructing a cladogram (text-fig. 10). Using *Stromatocystites* for outgroup comparison, as primitive, it is apparent that Bell's group Isorophina is based largely on symplesiomorphic characters and that the only possible synapomorphy that they share is the presence of four enlarged primordial cover plates, at least primitively. Of the two families included within the Isorophina, the Agelacrinitidae form a monophyletic group with the following autapomorphies: 1, hydropore structure formed of a large number of small plates, without a clearly differentiated hydropore plate; 2, ambulacral cover plates arranged in distinct cycles. The genus *Lispidecodus*, which Kesling (1967) considered to be sufficiently distinct to merit its own family, also belongs here in my opinion. The other family, Bell's Isorophidae, is paraphyletic as it lacks any unique synapomorphy.

Members of the second suborder, Lebetodiscina, share two good synapomorphies: 1, the loss of all secondary cover plates in all but the oral area; 2, having sutural passageways between adjacent cover plates. The great majority also possess enlarged primordial cover plates, especially in the C/D interray. In the family Carneyellidae the oral area is dominated by three large primordial cover plates; both the secondary cover plates and the shared oral cover plates have been lost from the oral area. The dominance of the primordial cover plates in the oral region and the extremely simple arrangement of ambulacral cover plates are features typical of juvenile lebetodiscinids and suggest that this family may have evolved through heterochrony. The Lebetodiscinae have a less well-differentiated peripheral rim than any other isorophid family, and this may be a shared derived character for the group.

Isorophids are usually considered to have evolved from edrioasterids (Bather 1915; Bockelie and Paul 1983), although Bell and Sprinkle (1978) thought that they were independently derived from some unknown Cambrian group. Some primitive isorophids such as *Savagella* retain a stout ring of marginal ossicles that are triangular in cross-section and very reminiscent of those in *Cambraster* and *Edriodiscus*. Isorophids also have a peripheral skirt of plates lying outside the marginal ring of ossicles, as found in *Edriodiscus*. These apomorphic features suggest that *Cambraster*, *Edriodiscus*, and isorophid edrioasteroids belong to the same clade. Jell *et al.* (1985) have recently reported an isorophid edrioasteroid from the Upper Cambrian of Australia, but this is too poorly preserved to add much to our understanding of their early evolution.

Cyclocystoids. This group has been revised and reinterpreted recently by Smith and Paul (1982). They chose to maintain cyclocystoids as a separate class but suggested that they were closely related to both *Cambraster* and isorophid edrioasteroids. Cyclocystoids are a rather peculiar and

TABLE 2. Analysis of character distribution within Bell's (1976) Order Isorophida. Synapomorphic characters 1–12 (see text-fig. 10) are in bold. Outgroup comparison has been made with Cambrian edrioasteroids.

Suborder LEBETODISCINA Bell, 1976	Suborder ISOROPHINA Bell, 1976
1. **Anal structure a periproct**	Anal structure a valvular cone
2. **Three oral primary cover plates enlarged** or none	3. **Four oral primary cover plates enlarged** or none
4. **Primary cover plates only**	Primary and secondary cover plates
5. **Cover plate sutural passageways**	No cover plate sutural passageways

Suborder ISOROPHINA Bell, 1976

Family ISOROPHIDAE Bell, 1976	Family AGELACRINITIDAE Chapman, 1860
Theca domal	Theca domal or clavate
Four primary oral cover plates	Four primary oral cover plates or none
Hydropore incorporated into central oral rise	6. **Hydropore structure isolated or semi-integrated; composed of many plates**
Cover plates alternately large and small	7. **Cover plates arranged in multiple cycles**
Interambulacra squamose and imbricate	Interambulacra squamose, imbricate or tesselate

Suborder LEBETODISCINA Bell, 1976

Family LEBETODISCIDAE Bell, 1976	Family CARNEYELLIDAE Bell, 1976
Theca domal, discoidal or clavate	Theca domal
Lateral shared cover plates present	8. **Lateral shared cover plates absent**
Secondary oral cover plates present	9. **Secondary shared cover plates absent**
10. **Hydropore plate adjacent to ambulacrum**	Hydropore plate forming part of oral area
Ambulacra high pronounced ridges	Ambulacra low and rounded
Cover plate passageways near vertical	Cover plate passageways oblique
11. **Peripheral plates squamose, marginals poorly differentiated**	Peripheral plates geniculate with differentiated marginals
Cover plates hardly differentiated in oral area	12. **Three very large primary cover plates in oral area**
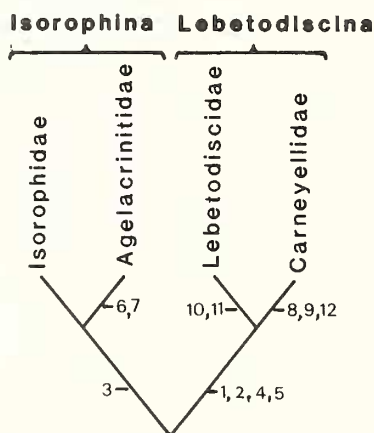
TEXT-FIG. 10. Cladogram of character distribution for the major groups within Bell's (1976) group Isorophida. Characters 1–12 are given in Table 2.

poorly understood group of echinoderms that have all been placed within the single family Cyclocystoididae. They share a number of unique characters which distinguish them from other echinoderms, including the possession of perforate marginal ossicles that have distal cupules roofed over by a movable peripheral skirt of plates, a dorsal plated surface composed of annular plates with a polygonal outline, and the absence of a ventral periproct. However, they share with *Cambraster*, *Edriodiscus*, and isorophids such as *Savagella* the ring of stout marginal ossicles and the peripheral skirt of plates; they share uniserial ambulacral flooring plates with isorophids alone. This suggests that cyclocystoids and isorophids are sister groups.

Cyathocystids. *Cyathocystis* and *Cyathotheca* are two very distinctive genera that were placed in their own family Cyathocystidae by Bather (1899). Although Bell (1980) suggested that *Tinneischytes* and *Hadrochthus* should also be included in this family, Bockelie and Paul (1983) convincingly demonstrated that they did not belong here and were in fact isorophids. Bockelie and Paul (1983) identified a number of autapomorphies for this group: 1, the dorsal surface is a single calcite element which is cup-shaped and moulded to the substratum; 2, the five primordial cover plates remain in contact throughout growth; 3, a single large deltoid plate occupies each interambulacral zone; 4, there are no ambulacral flooring plates. They therefore suggested that cyathocystids represented a line of descent from *Stromatocystites* independent of the main edrioasterid–isorophid lineage.

Not all of their supposed synapomorphies are unique to this group, however, since the five primordial cover plates also remain in contact throughout growth in pyrgocystids (text-fig. 11) and pyrgocystids also possess only a single interradial plate in each interambulacrum. Furthermore, the fact that these deltoid plates surround the peristome, abut along the distal edge at the perradial suture, and carry articulating cover plates strongly indicates that these are homologous not with interambulacral plates but with the fused ambulacral mouth frame plates present in *Cambraster*, *Totiglobus*, and edrioasterids. Bockelie and Paul (1983) were therefore mistaken in suggesting that cyathocystids lacked flooring plates; rather they have lost all but the most proximal fused ambulacral flooring plates that form the mouth frame elements. Cyathocystids are so highly modified that their precise phylogenetic position is difficult to ascertain. However, the presence of oral frame elements composed of fused ambulacral flooring plates is a synapomorphy shared with both edrioasterids and the *Cambraster*-isorophid clade. In the cladogram they are therefore placed in a trichotomy with these two groups (text-fig. 12).

Pyrgocystids. Pyrgocystids are fully plated and turret-shaped edrioasteroids with an elongate stalk composed of imbricate dorsal plates and a small ventral surface surmounting the stalk (text-fig. 11). The marginal ossicles lie at the top of the turret and surround the ventral surface. On each marginal plate there is a pair of internal processes similar to those in *Totiglobus* (text-fig. 11). These were presumably attachment sites for the dorsal muscles responsible for contraction of the turret. In some there is a basal sac of minute platelets embedded in a coriaceous membrane. Unfortunately very little is known about the plating of the ventral surface. A single large interradial plate lies in each interambulacrum except posteriorly, where a small number of smaller plates are found (see Holloway and Jell 1984). Pyrgocystids have tall, narrow cover plates very much like those of cyathocystids; the primordial cover plates meet above the oral area (text-fig. 11B), also like cyathocystids. If, as in cyathocystids, the large interradial 'deltoid plates' turn out to be mouth frame plates formed through fusion of proximal flooring plates, as is strongly suspected, then cyathocystids and pyrgocystids are best considered to be sister taxa. The perradial margin of the deltoid plates is scalloped exactly as in cyathocystids and no flooring plates have yet been seen in partially disarticulated specimens. Both groups have the same turret-shaped theca and almost identical cover plate arrangements. The principal difference is that in cyathocystids dorsal plating is formed of a single calcite element, whereas in pyrgocystids it is composed of many plates. Possibly dorsal plating in cyathocystids has become fused.

Text-fig. 12 provides a character matrix for the various groups of edrioasteroid discussed above and a summary of their relationships derived from cladistic analysis of this matrix.
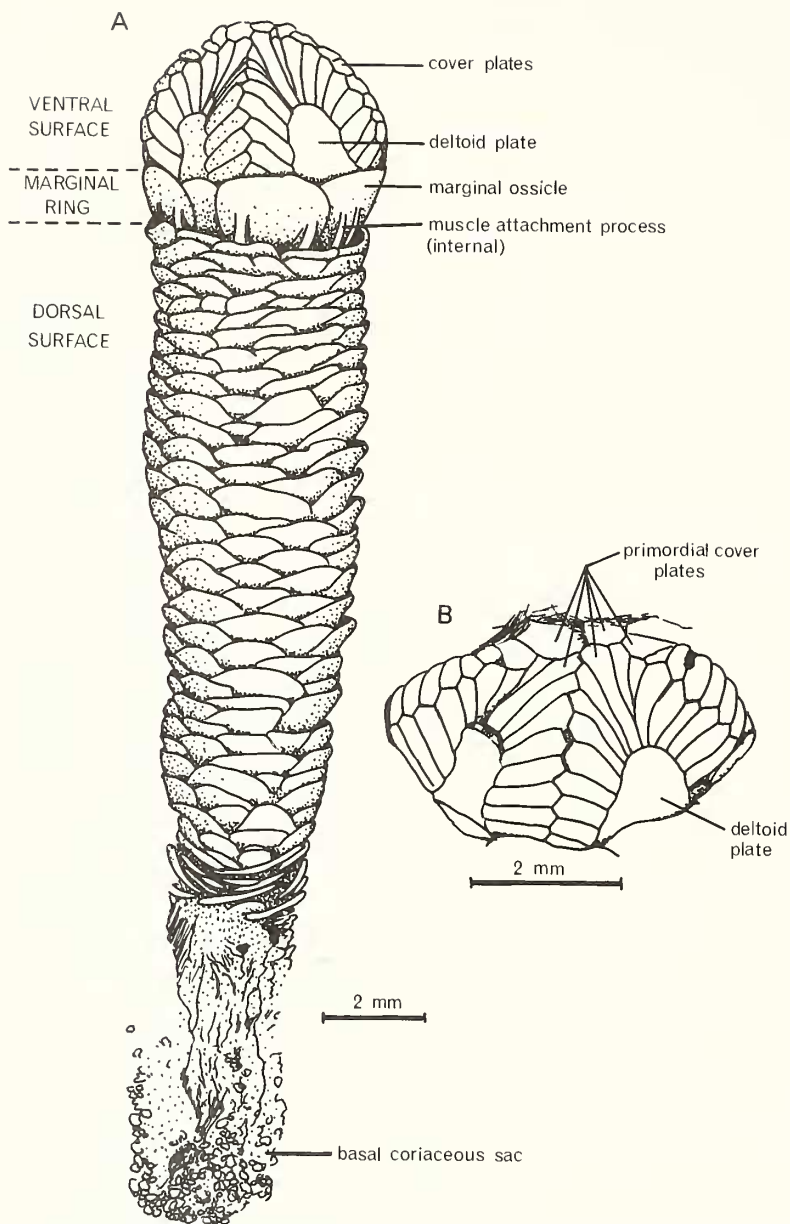
TEXT-FIG. 11. *Rhenopyrgus grayae* (Bather), BM(NH) E23470, Ashgill, Upper Ordovician, Girvan, Scotland; camera lucida drawings of the holotype to show the basic morphological features of pyrgocystids: A, lateral; B, oral surface.

CLASSIFICATION

Edrioasteroids have always been considered a natural grouping and, since 1899, have been assigned the status of class (Bather 1899). However, current classification schemes of this group, such as those of Bell (1980), do not reflect the hierarchical groupings identified in the preceding section and summarized in text-fig. 12. It is therefore necessary to rationalize the classification as a whole in order to place the Cambrian genera into their appropriate monophyletic groups. If the characters used to define edrioasteroids are examined critically, it is difficult to identify any advanced characters that are not also present in other primitive eleutherozoan groups. Instead, edrioasteroids are characterized by having retained primitive features of crown-group echinoderms, such as the ventral periproct, unmodified ambulacral cover plates, an oral mouth frame that is fixed, and an attached mode of life as adults; but they lack the pelmatozoan synapomorphies of a dorsal stem and an exothecal ambulacral subvective system. Having interradial mouth frame elements formed by fusion of proximal ambulacral flooring plates is an important shared derived character that unites *Totiglobus*, *Cambraster*, edrioasterids, cyathocystids, and probably pyrgocystids but which is not found in *Stromatocystites* or primitive asteroids and ophiuroids. This implies that all edrioasteroids, with the exception of *Stromatocystites*, form a natural clade which can be considered as a plesion within the stem group of the Eleutherozoa (see Smith 1984*b*). As this plesion corresponds more or less to the class Edrioasteroidea Bather as currently accepted (though with the removal of *Stromatocystites* and the inclusion of cyclocystoids), this seems the obvious name and taxonomic rank to maintain, respecting historical tradition. *Stromatocystites* is then the primitive sister group to all other known eleutherozoan echinoderms and is best classified as a separate and distinct plesion.

Within the plesion Edrioasteroidea there are three subgroups forming a trichotomy in the cladogram (text-fig. 12). At present, there are insufficient morphological data to solve this trichotomy convincingly and the three groups identified are best assigned equal rank, even though two of them contain just four genera each whereas the third contains some thiry-five genera and is considerably more diverse. This last group includes *Cambraster*, Bell's Isorophida, and cyclocystoids. Cyclocystoids have in recent years been separated off at class level, even though the few genera known all belong to a single family, the Cyclocystoididae. Similarly, isorophids, as defined by Bell (1976), display an extremely limited range of morphological variation and are a very conservative group. Bell (1976) elevated this group to the rank of order, recognizing two suborders each with two families. However, in comparison with taxonomic assignment in other echinoderm groups, Bell's order Isorophida is more comparable to a family, and the various subdivisions to subfamilies and tribes. It might be more sensible therefore to reduce Bell's Isorophida to a lower rank such as family, where the name Agelacrinitidae Chapman 1860 would have priority. The two suborders erected by Bell could then be transformed to the rank of subfamily; Lebetodiscinae (for the Lebetodiscina) and Isorophinae (for the Isorophina). This would make cyclocystoids and the Agelacrinitidae sister groups. Although *Cambraster*, cyclocystoids, and agelacrinitids differ in a number of striking features, they appear to form a monophyletic group and should therefore be classified together. Taxonomic debasement can be avoided by uniting them within one order and the most obvious available name for this group is the order Isorophida. This then requires the expansion of Bell's original diagnosis for the Isorophida to include the cyclocystoids and *Cambraster*.

If this clade is assigned the rank of order, then the two other monophyletic sister groups should also be ranked as orders. There is already an order Edrioasterida for the genera *Edrioaster*, *Edriophus*, and *Totiglobus*; it is only necessary to include *Walcottidiscus* here and expand the diagnosis for the family Edrioasteridae in consequence. An order Cyathocystida is also currently available, although at present it contains only the single family Cyathocystidae. If the pyrgocystids are correctly interpreted as the sister group to the cyathocystids then the Cyathocystida needs to be redefined to contain two families, the Pyrgocystidae and the Cyathocystidae.

A phylogenetic classification of the plesion Edrioasteroidea, using the conventions recommended by Wiley (1979), is presented in Table 3, together with a more traditional scheme for comparison. The precise taxonomic levels that have been chosen are, and always will be, open to dispute, but they are

TABLE 3. Classification of the Edrioasteroidea.

| Traditional classification (based on Bell 1980, but with later additions)	Revised classification (this paper)
Order STROMATOCYSTITOIDA Termier and Termier, 1969	Genus STROMATOCYSTITES Pompeckj, 1896
Family STROMATOCYSTITIDAE Bassler, 1936	Plesion (Class) EDRIOASTEROIDEA Billings, 1858
Family CAMBRASTERIDAE Termier and Termier, 1969	Order EDRIOASTERIDA Bell, 1976 (sedis mutabilis)
Order EDRIOASTEROIDA Bell, 1976	Family TOTIGLOBIDAE Bell and Sprinkle, 1978
Family EDRIOASTERIDAE Bather, 1898	Family EDRIOASTERIDAE Bather, 1898
Family TOTIGLOBIDAE Bell and Sprinkle, 1978	Order ISOROPHIDA Bell, 1976 (emend.) (sedis mutabilis)
Order ISOROPHIDA Bell, 1976	Genus CAMBRASTER Cabibel, Termier and Termier, 1958
Suborder LEBETODISCINA Bell, 1976	Genus EDRIODISCUS Smith, 1985
Family LEBETODISCIDAE Bell, 1976	Family CYCLOCYSTOIDIDAE Miller, 1882
Family CARNEYELLIDAE Bell, 1976	Family AGELACRINITIDAE Chapman, 1860
Suborder ISOROPHINA Bell, 1976	Subfamily ISOROPHINAE Bell, 1976
Family HEMICYSTITIDAE Bassler, 1936 (= ISOROPHIDAE Bell, 1976)	Subfamily LEBETODISCINAE Bell, 1976
Family AGELACRINITIDAE Chapman, 1860	Order CYATHOCYSTIDA Bockelie and Paul, 1983 (emend.) (sedis mutabilis)
Suborder UNCERTAIN	Family PYRGOCYSTIDAE Kesling, 1967
Family PYRGOCYSTIDAE Kesling, 1967	Family CYATHOCYSTIDAE Bather, 1898
Family LISPIDECODIDAE Kesling, 1967	
Family RHENOCYSTIDAE Holloway and Jell, 1984	
Order CYATHOCYSTIDA Bockelie and Paul, 1983	
Family CYATHOCYSTIDAE Bather, 1899	

the least important part of the classification scheme. It is the hierarchical and listing orders that convey information and on which the classification should be judged.

Emended taxonomic definitions

Plesion (Class) EDRIOASTEROIDEA Billings, 1858. Stem group eleutherozoans with a fixed mouth frame of ambulacral flooring plates (primitively five interradial elements). Retained plesiomorphic characters include the sessile mode of life as adults, the periproct opening ventrally in the posterior interambulacrum, and a largely unmodified arrangement of cover plates protecting the ambulacral groove.

Order EDRIOASTERIDA Bell, 1976. Sub-globular edrioasteroids with biserial flooring plates, a dorsal surface that is reduced relative to the ventral surface, and ambulacra that extend sub-ambitally.

TEXT-FIG. 12. Character distribution and the derived cladogram for principal edrioasteroid groups. Characters 1–22 are as follows: 1, oral frame composed of fused ambulacral flooring plates positioned interradially, transformed to oral frame of radially positioned flooring plates; 2, loss of epispires from interambulacral zones; 3, dorsal growth retarded relative to ventral growth; 4, ambulacral tips free of the marginal ring; 5, central part of dorsal surface uncalcified; 6, ambulacra curve around ambitus; 7, dorsal surface a tiny, plated suction pad; 8, five radial elements in oral frame in addition to the fused flooring plates; 9, secondary cover plates greatly reduced or lost; 10, anal structure a periproct; 11, all five primordial cover plates meet centrally; 12, single large deltoid (= fused ambulacral flooring plates?) occupies interambulacral zones; 13, dorsal surface expanded into a stalk; 14, dorsal surface a single (?fused) calcite element; 15, marginal ossicles stout, forming a distinct frame to the ventral surface; marginal ossicles as imbricate ring (reversed character state); 16, marginal ossicles inserted into the dorsal pavement to form a clearly demarcated peripheral skirt; 17, flooring plates uniserial; 18, loss of sutural pores for internal ampullae; 19, perforate marginal ossicles; 20, dorsal plates annular with central perforation; 21, peripheral skirt modified into a protective canopy for the cupule zone; 22, cover plates extend intrathecally at the interradial suture to conceal the flooring plates externally.
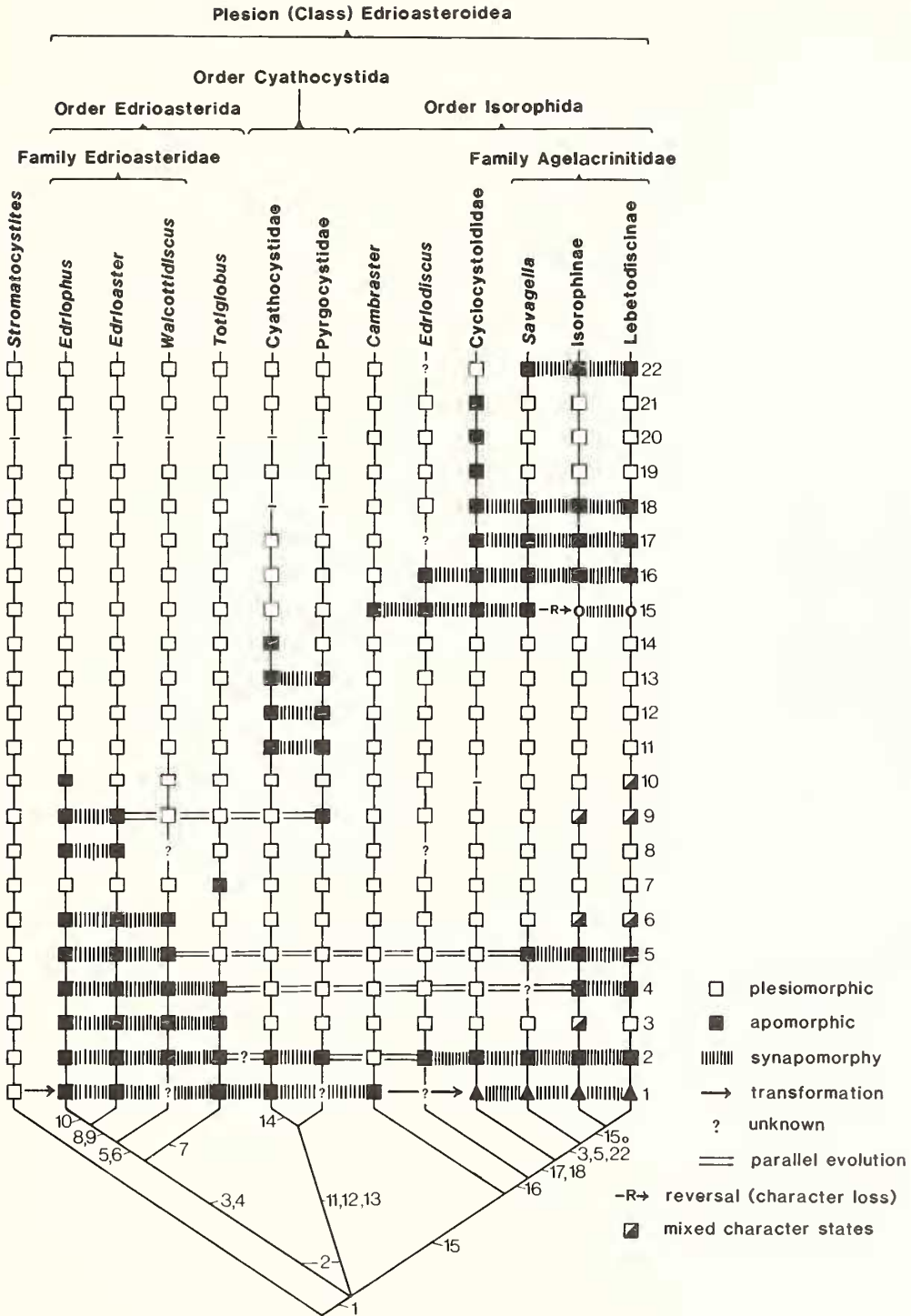
Order CYATHOCYSTIDA Bockelie and Paul, 1983. Turret-shaped edrioasteroids with a greatly expanded dorsal surface, a single large deltoid plate in each interambulacrum (fused ambulacral flooring plate?), and primordial ambulacral cover plates that meet above the peristome. The dorsal stalk may be either multiplated or composed of a single (?fused) calcite element.

Order ISOROPHIDA Bell, 1976. Discoidal to clavate edrioasteroids with a distinct peripheral rim of plates extending beyond the ring of marginal plates.

Family AGELACRINITIDAE Chapman, 1860. Isorophids with uniserial flooring plates and generally unbranched arms, cover plates with adradial intrathecal extensions that conceal the flooring plates externally, and an uncalcified dorsal surface within the peripheral skirt.

Subfamily LEBETODISCINAE (= Suborder LEBETODISCINA Bell, 1976). Agelacrinitids with sutural passages between adjacent cover plates.

Subfamily ISOROPHINAE (= Suborder ISOROPHINA Bell, 1976). Agelacrinitids with primary ambulacral cover plates in two or more sizes, arranged cyclically, and primitively with four enlarged primordial cover plates.

SYSTEMATIC PALAEONTOLOGY

Repositories of specimens referred to below are abbreviated as follows: BM(NH), British Museum (Natural History), London; CPC, Commonwealth Palaeontological Collections, Bureau of Mineral Resources, Canberra, Australia; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; NYSM, New York State Museum, Albany; USNM, United States National Museum, Smithsonian Institution, Washington D.C.

Genus STROMATOCYSTITES Pompeckj, 1896

    1896   *Stromatocystites* Pompeckj, p. 506.
    1899   *Stromatocystites* Pompeckj; Jaekel, p. 42.
    1900   *Stromatocystites* Pompeckj; Bather, p. 206.
    1911   *Chilocystis* Perner Mss; Zelizko, p. 6.
    1918   *Stromatocystites* Pompeckj; Jaekel, p. 112.
    1919   *Stromatocystites* Pompeckj; Schuchert, p. 1.
    1936   *Stromatocystites* Pompeckj; Bassler, p. 3.
    1966   *Stromatocystites* Pompeckj; Regnéll [*pars*], p. U133.
    1969   *Stromatocystites* Pompeckj; Termier and Termier, p. 133.
non 1905   *Stromatocystites* Miquel, p. 476 [= *Cambraster*].

Diagnosis. Theca flattened, discoidal, or weakly pentagonal in outline and fully plated; ambulacra straight, reaching edge of ventral surface; cover plates arranged as multiserial sheets; interambulacral plates with sutural epispires; dorsal plating polygonal, tesselate, with large centro-dorsal.

Type species. Stromatocystites pentangularis Pompeckj, 1896, by original monotypy.

Other species. S. walcotti Schuchert, 1919.

EXPLANATION OF PLATE 87

Figs. 1–6. *Stromatocystites pentangularis* Pompeckj, 1896. 1, 2, and 5, BM(NH) E16004, Middle Cambrian, Jince, Czechoslovakia: 1, general view showing three individuals, two of which are dorsal surface uppermost, ×1; 2, one individual, ventral surface uppermost, ×2; 5, same individual, dorsal surface, ×2. 3 and 4, BM(NH) E29830, Lower Cambrian, Bonne Bay, Newfoundland: 3, oral, ×2; 4, aboral, ×2. 6, specimen in the collection of Dr Krantz of Bonn, latex BM(NH) E63138, Middle Cambrian, Pod Trnim, Czechoslovakia, dorsal surface, ×2.

All photographs are of latex casts whitened with ammonium chloride sublimate.

PLATE 87

SMITH, *Stromatocystites*

Stratigraphical age and distribution. Uppermost Lower Cambrian (*Olenellus* Beds) to Middle Cambrian (*Paradoxides gracilis* Zone) from Jince, Czechoslovakia, Bonne Bay, Newfoundland, and Rostock, northern Germany (in glacial drift, presumably derived from Scandinavia).

Remarks. *Stromatocystites* was first described by Pompeckj in 1896 and his figures have been copied by all later workers. *S. pentangularis* and *S. walcotti* are each known from a large number of specimens and are redescribed below. A third species, *S. balticus* Jaekel, 1899, is represented by only two specimens whose whereabouts are no longer known and it is treated as a *nomen dubium*.

Stromatocystites is distinguished from other Cambrian edrioasteroids by having dorsal and ventral surfaces similar in size, sutural epispires in interambulacral zones, straight narrow ambulacra with multiserial cover plate sheets, poorly developed marginal ring plates, and simple unfused oral frame plates. *Cambraster* likewise has interambulacral epispires but differs in having compound oral frame plates and a stout marginal ring of ossicles. *Walcottidiscus* and *Totiglobus* both lack epispires and have a reduced dorsal surface.

Stromatocystites is stratigraphically the oldest known genus of eleutherozoan echinoderm.

Stromatocystites pentangularis Pompeckj, 1896

Plate 87; Plate 89, fig. 1; text-figs. 5, 6в, с, 13–15

1896   *Stromatocystites pentangularis* Pompeckj, p. 506, pl. 13, figs. 1–6.
1899   *Stromatocystites pentangularis* Pompeckj; Jaekel, p. 42, figs. 5–8.
1900   *Stromatocystites pentangularis* Pompeckj; Bather, p. 206, fig. 1.
1911   *Chilocystis bohemica* Perner Mss, *in* Zelizko, p. 6.
1919   *Stromatocystites pentangularis* Pompeckj; Schuchert, p. 2, fig. 1е.
1936   *Stromatocystites pentangularis* Pompeckj; Bassler, p. 3, pl. 1, figs. 6 and 7.
1958   *Stromatocystites pentangularis* Pompeckj; Cabibel, Termier and Termier, p. 283, fig. 2.
1966   *Stromatocystites pentangularis* Pompeckj; Regnéll, p. U160, text-fig. 126.
1969   *Stromatocystites pentangularis* Pompeckj; Termier and Termier, p. 133, figs. 1–3.

Diagnosis. A species of *Stromatocystites* with a domed ventral surface and pentagonal outline; marginal ossicles undifferentiated; ambulacra narrow, without V-shaped intrathecal extensions; centro-dorsal plate surrounded by six or seven plates; oral frame large, pentagonal.

Types. Pompeckj (1896) based his description on forty examples from 'Pod Trnim bei Tejrovic' of which six were illustrated. These were stated to belong to the Geologischen Reichsanstalt, Vienna, but are now housed in the Czechoslovakian Geological Survey, Prague. No holotype was designated by Pompeckj, thus all are syntypes. The holotype of *Chilocystis bohemica* is P/77916, Národní Muzeum, Prague; a cast, BM(NH) E16008, of this specimen was studied (Pl. 89, fig. 1).

Material studied. The following description is based largely on eighteen well-preserved individuals, BM(NH) E15897, E15898, E16004, and E29380, and on the two individuals, USNM 56665. The collections in the Národní Muzeum, Prague, have also been studied, as have three latex casts of specimens in the private collection of Dr Krantz of Bonn, kindly given to me by Professor Ubaghs (BM(NH) E63137–63139).

Stratigraphical age and distribution. BM(NH) E29380 (four individuals) comes from the *Olenellus* Beds, Taconian, high Lower Cambrian of Bonne Bay, Newfoundland. Other material comes from the *Paradoxides gracilis* Zone, Upper Jince Beds, Middle Cambrian of Tyrovic and Jince, Czechoslovakia.

Description. All specimens examined are preserved as natural moulds of external surfaces. The theca is pentagonal in outline with the ambulacra running to the five rounded corners. In a number of specimens the interambulacral portions are gently concave suggesting that there may have been internal radially arranged postural muscles present. The entire theca is plated. On the ventral surface the ambulacra form narrow ridges which extend to the margin. These meet centrally in a 2 : 1 : 2 pattern with ambulacra B + C and D + E paired and united on either side of the mid-line. Ambulacrum A is unpaired and set almost at right angles to the paired lateral ambulacra (text-fig. 15). The ambulacra form prominent ridges on the theca while interambulacral zones are generally depressed. The ambulacra are straight and composed of biserial flooring plates with left and right cover plate series. Flooring plates are relatively short (in the perradial/interradial direction) and broad (in the

TEXT-FIG. 13. *Stromatocystites pentangularis* Pompeckj, 1896, BM(NH) E16008, camera lucida drawing, showing the ventral plating in one interambulacrum.

flooring plate

primary cover plate

2 mm
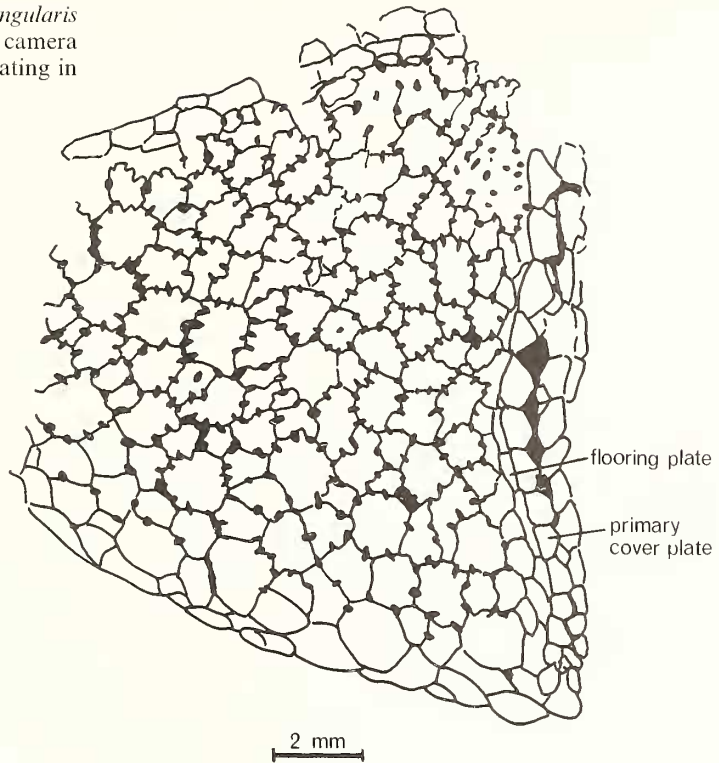
adoral/adambital direction) (text-fig. 6B, C). The perradial edge of each plate is weakly angled and the flooring plates alternate to produce a zigzag perradial suture. Interradially a small part of the flooring plate is exposed between the interambulacral plates and the cover plate sheets. On the adoral/adambital suture, immediately perradial to the site where the cover plates attach, is a small ovoid pore, shared equally between the two flooring plates. The flooring plates appear to be steeply inclined so as to form a deep and narrow ambulacral tunnel.

Cover plates are arranged as two multiserial sheets that attach towards the adradial edge of the flooring plates, one on either side of the ambulacrum. A large pentagonal primary cover plate rests directly on each flooring plate. Between these, more or less directly above the flooring plate sutures, are smaller diamond-shaped cover plates. A further two or so irregular rows of small cover plates lie above the primary and diamond-shaped cover plates (text-fig. 14). The two cover plate sheets meet along the mid-line and, in well-preserved material, form a crenulated crest to the ambulacral ridge. In the oral area the arrangement of cover plates appears identical with that of the more distal ambulacral areas and there are no distinguishably larger plates. The flooring plates and cover plate series are more or less identical to those in helicoplacoids (see Paul and Smith 1984).

In almost all specimens compaction has pressed dorsal and ventral surfaces together so that narrow ridges mark the position of the underlying flooring plates on the dorsal surface. The five ridges do not meet in a 2:1:2 pattern, as might be expected, but bifurcate near the centre and unite interradially to form a pentastellate ring (Pl. 87, figs. 4–6). This suggests that adorally the individual columns of flooring plates could have separated along the perradial suture and that the most proximal flooring plates were united interradially to form a large and flexible peristomial opening, as in primitive asteroids. Unfortunately, no specimens examined showed the internal face of the ventral surface and the precise arrangement of flooring plates in the oral region must remain speculative.

Interambulacral zones on the ventral surface are composed of small polygonal and tesselate plates of variable size and shape (text-fig. 13). There are up to fifteen plates abreast in an interambulacral zone. At the sutures between plates there are small oval or slit-like epispires with neither internal nor external rims. Epispires are absent from a narrow zone bordering the ambulacra and immediately adjacent to the marginal plates. The periproct lies more or less centrally in the C/D interray. It is composed of about twelve to fifteen lath-shaped
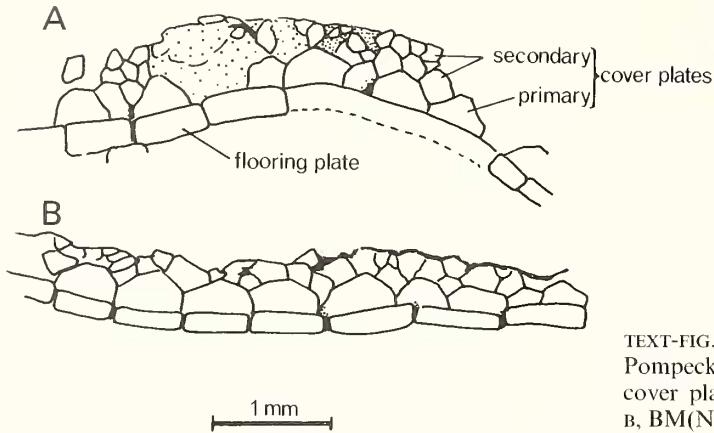
TEXT-FIG. 14. *Stromatocystites pentangularis* Pompeckj, 1896, camera lucida drawings of cover plate arrangements: A, USNM 56665b; B, BM(NH) E16004.

plates arranged radially. These plates and those immediately adjacent lack epispires. They generally lie more or less flush with the surrounding interambulacral plates.

No third aperture has been identified amongst the plates of the oral area, probably because no specimen is sufficiently well preserved in this region to reveal such a structure. The dorsal surface is usually concave and pressed against the ventral surface, although in life it was presumably more or less flat. All specimens show a sharp marginal rim suggesting that the large marginal plates formed a more rigid frame, as in *S. walcotti*. Immediately inside this rim there is a very narrow zone of tiny plates. The remainder of the dorsal surface is covered in polygonal, tesselate plates with a pitted surface texture. These plates are more or less irregularly arranged (text-fig. 5B), but a large equant plate at the centre of the disc is surrounded by six or seven other large plates. There is no evidence for any attachment structure by which adult *Stromatocystites* might have attached itself to a hard substratum.

Remarks. S. pentangularis is not uncommon at certain horizons and clusters of individuals are preserved together on bedding surfaces. As individuals showing both dorsal and ventral surfaces are found together on the same slab, they probably represent individuals that have been current transported and buried alive. The original description by Pompeckj (1896) was fairly good and, for the most part, later workers have simply repeated his findings without adding any new information.

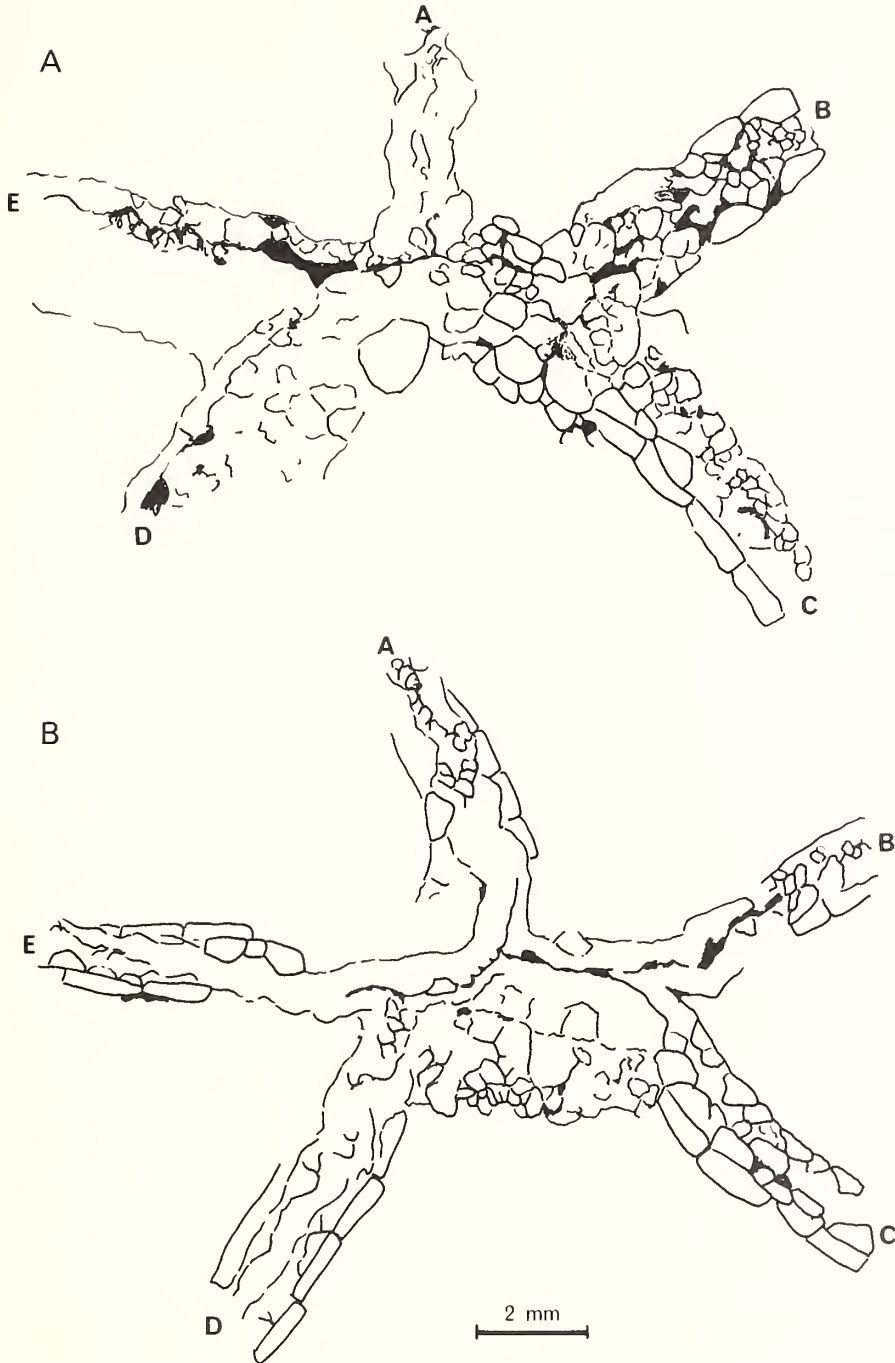### *Stromatocystites walcotti* Schuchert, 1919

Plate 88; text-figs. 4, 7, 16

1919   *Stromatocystites walcotti* Schuchert, p. 3, pl. 7, figs. 1–3; text-fig. 1.
1966   *Stromatocystites walcotti* Schuchert; Regnéll, p. U160, text-fig. 126.
1969   *Stromatocystites walcotti* Schuchert; Termier and Termier, p. 137, pl. 8, figs. 1–4.
1984   *Stromatocystites walcotti* Schuchert; Paul and Smith, p. 452, text-figs. 6 and 7.

Diagnosis. A species of *Stromatocystites* discoidal in shape and with a pentagonal outline; marginal ring plates present and visible externally; ambulacral flooring plates with V-shaped intrathecal extensions; oral frame not large and pentastellate; centro-dorsal plate surrounded by a circle of ten or eleven plates.

Types. Holotype, USNM 66443 (Pl. 88, fig. 1); paratypes, USNM 66444.

Material examined. In addition to the holotype and paratypes, twenty slabs, USNM 376690 and 384978–384984, with a total of thirty-seven individuals have been examined.

Stratigraphical age and distribution. Olenellus Beds, Taconian, upper Lower Cambrian; all specimens come from the eastern arm of Bonne Bay, western coast of Newfoundland.

TEXT-FIG. 15. *Stromatocystites pentangularis* Pompeckj, 1896, camera lucida drawings of plating in the oral area: A, USNM 56665b; B, BM(NH) E16004.
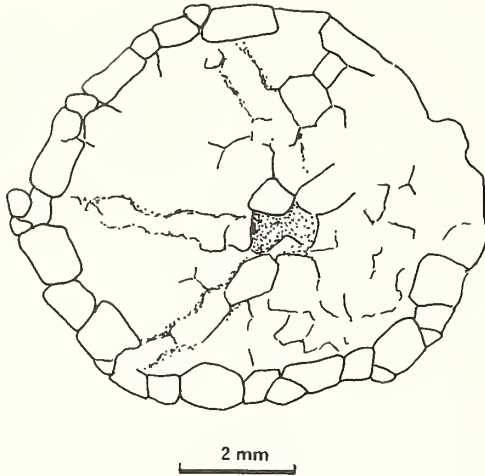
TEXT-FIG. 16. *Stromatocystites walcotti* Schuchert, 1919, USNM 384978, camera lucida drawing of the dorsal plated surface of a juvenile showing the prominent marginal ring plates.

2 mm

Description. Specimens are 9–22 mm in diameter, weakly pentagonal in outline, and have a flattened profile without the ventral convexity characteristic of *S. pentangularis*. Ambulacra are long and straight and form ridges on the ventral surface. They extend to the ambitus and the tip of each ambulacrum is inserted between the large plates forming the marginal ring. Flooring plates are short and broad and are arranged alternately in two columns with a weakly zigzag perradial suture. Each plate appears to have a pair of short processes that extend intrathecally, but is otherwise very like those of *S. pentangularis*. The arrangement of cover plates is not clearly seen in any of the specimens, but it is quite obviously a multiplated sheet. The ambulacra meet in a 2 : 1 : 2 pattern over the oral area and there is no apparent differentiation of the cover plates in this region. The internal aspect of the ventral surface is seen in USNM 376690 and shows the oral frame. The oral frame is transversely elongate and made up of the ten most adoral unfused flooring plates, together with one large asymmetrical inter-ambulacral plate in the C/D interray (the hydropore plate) (text-fig. 7). Unlike *S. pentangularis*, *S. walcotti* shows no evidence of having perradial slits and a flexible mouth frame. There is no obvious hydropore groove in the mouth frame, such as is found in agelacrinitids, but the large hydropore plate is embayed on the D ray side, possibly to allow passage for some soft tissue structure.

The interambulacral zones of the ventral surface are composed of irregularly arranged polygonal plates with epispires. Individual plates are comparatively larger and fewer in number than in *S. pentangularis*, with up to eight plates abreast in any one interambulacrum. The periproct opens in the C/D interray close to the ventral margin and slightly offset towards the C ray. It consists of a large number of elongate plates arranged more or less radially. The periproct is always flush with the surrounding interambulacral plating.

Marginal plating is more strongly developed than in *S. pentangularis* and is sometimes the only part to be preserved. There is a ring of abutting plates which are thickened along the dorsal facing edge. They are held nearly perpendicular to the sea floor around the margin of the theca.

The dorsal surface is covered by a pavement of polygonal, tesselate plates, except immediately adjacent to the marginal ossicles where there are two or three irregular rows of small, loosely fitting plates. At the centre of the disc there is a large, almost circular centro-dorsal plate surrounded by a ring of ten or eleven large, radially elongate plates. Elsewhere the dorsal plating is somewhat smaller and totally irregular in its arrangement.

EXPLANATION OF PLATE 88

Figs. 1–5. *Stromatocystites walcotti* Schuchert, 1919. 1, USNM 66443, holotype, Lower Cambrian, Bonne Bay, Newfoundland; dorsal surface (see text-fig. 4), × 2·5. 2, USNM 384978, Lower Cambrian, Bonne Bay, Newfoundland; dorsal surface of a juvenile showing the prominent marginal ring at this stage, × 5. 3–5, USNM 376690, no locality data: 3, general view of the interior of the ventral surface, × 1·8; 4, detail of the periproct and ambulacral flooring plates (internal), × 4; 5, detail of the oral frame, × 5.

All photographs are of latex casts whitened with ammonium chloride sublimate.
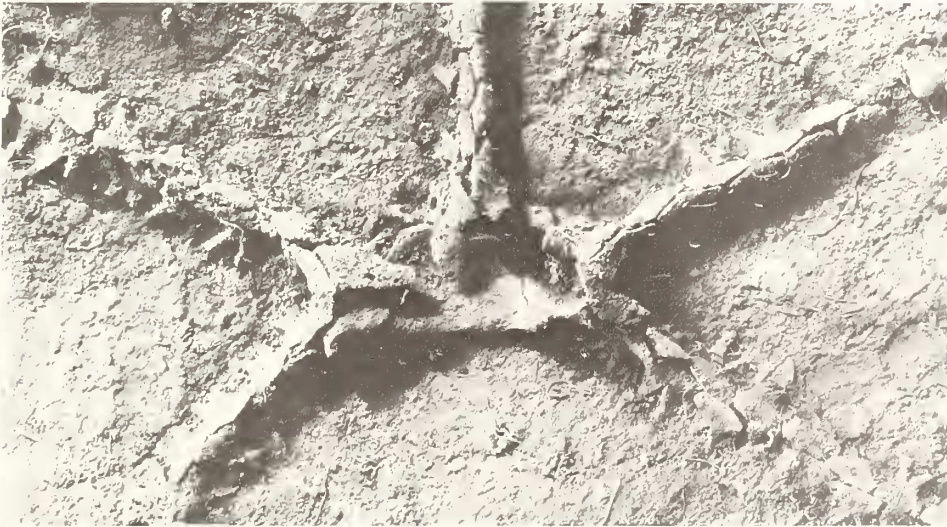
PLATE 88

SMITH, *Stromatocystites*

Remarks. The original description by Schuchert (1919) is accurate in most respects. Schuchert used the name *S. walcotti* for six larger specimens (including the holotype) but placed all the smaller specimens in a different group which he designated as variety *minor*. As the two forms are indistinguishable and simply represent individuals at different growth stages, Schuchert's variety is not a biologically useful concept.

S. walcotti is similar to *S. pentangularis* in many respects, but is less inflated ventrally, has a smaller, more transversely elongate mouth frame, and has a larger number of dorsal plates in contact with the centrodorsal. Termier and Termier (1969) believed that they could recognize inhalent orifices at the ambulacral tips, suggesting that the ambulacral passageways were enclosed and only opened to the exterior via these terminal orifices. In my opinion such openings did not exist in life and the Termiers were misled by one specimen in which the very terminal cover plates had been displaced during burial and compaction in a couple of the ambulacra.

S. walcotti was tentatively assigned to the genus *Cambraster* by Jell *et al.* (1985) because *C. tastudorum* and *S. walcotti* have rather similar dorsal plating, and *S. walcotti* is supposed to have a ring of marginal ossicles like *Cambraster*. Although marginal ossicles are present in *S. walcotti* and are more prominent than in *S. pentangularis*, particularly in juveniles, they appear to be much less well developed than they are in *Cambraster*. Furthermore, the development of a central zone of large polygonal plates on the dorsal surface is not restricted to *Cambraster* and *S. walcotti* but is also a feature of *S. pentangularis* (see Pl. 87). Therefore, although *S. walcotti* may well be directly ancestral to *C. tastudorum*, it lacks crucial features (such as a marginal skirt and stout marginal ring) that characterize *Cambraster* and cannot be placed within this genus.

Stromatocystites balticus Jaekel, 1899

Remarks. This species was erected on the basis of two specimens, both of which have since been lost. Jaekel's original description is rather vague and the distinction between this species and *Stromatocystites pentangularis* is not at all clear. Regnéll (1945) has reviewed all that is known about this species and I can add nothing else. Since no specimens now exist and the original description is too generalized to distinguish *S. balticus* from *S. pentangularis*, I recommend that *S. balticus* be treated as a *nomen dubium*. The original specimens came from the Middle Cambrian *Paradoxides paradoxissimus* Zone of the Baltic and were collected from a glacial erratic block in northern Germany.
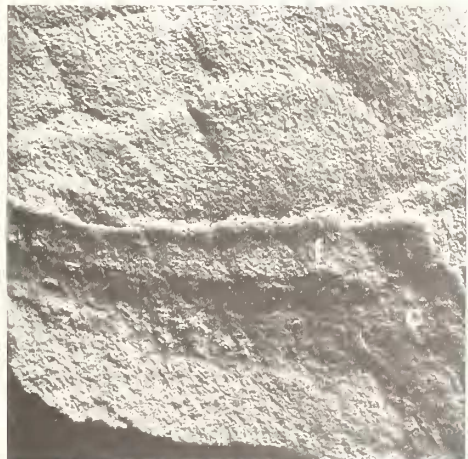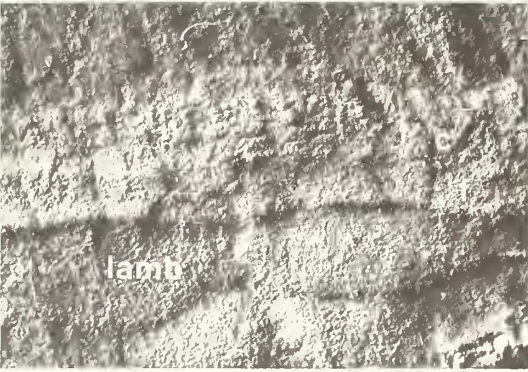
Genus WALCOTTIDISCUS Bassler, 1935

1935   *Walcottidiscus* Bassler, p. 3.
1936   *Walcottidiscus* Bassler; Bassler, p. 2.
1943   *Walcottidiscus* Bassler; Bassler and Moody, p. 209.
1966   *Walcottidiscus* Bassler; Regnéll, p. U161.

Diagnosis. Theca sub-ovoid, circular to roundedly pentagonal in outline; dorsal surface relatively small compared to ventral surface, consisting of an outer zone of tiny platelets and a central uncalcified zone; ambulacra curving sinistrally at the ambitus, extending sub-ambitally, composed of

PLATE 89

SMITH, *Stromatocystites, Walcottidiscus*

biserial flooring plates and multiserial cover plate sheets; interambulacral areas subtesselate, lacking epispires; periproct subambital.

Type species. Walcottidiscus typicalis Bassler, 1935, by original monotypy.

Stratigraphical age and distribution. Middle Cambrian Burgess Shale, *Bathyuriscus-Elrathina* Zone, British Columbia, Canada.

Remarks. Bassler (1935) described and figured a small edrioasteroid from the Burgess Shale under the name *W. typicalis.* His description was rather sketchy and, in places, somewhat misleading; the specimen has not since been redescribed. A year later, Bassler (1936) described a second specimen from the same locality under the name *W. magister.* This is a much larger specimen and superficially seems to be quite distinct. However, the differences between the two specimens are almost certainly a result of size; I interpret *W. typicalis* as a juvenile and *W. magister* as an adult of the same species.

    Neither specimen is particularly well preserved and details of ambulacral plating around the oral area cannot be made out. *Walcottidiscus* has certain characteristics that distinguish it from all other Cambrian edrioasteroids but which it shares with the Ordovician edrioasterids *Edrioaster* and *Edriophus.* These include the sub-oval shape, the strongly curved ambulacra that run around the ambitus, and the reduced dorsal surface with its central uncalcified zone. *Walcottidiscus* differs from both *Edrioaster* and *Edriophus* in the arrangement of ambulacral cover plates. In *Edrioaster* and *Edriophus* there is a series of large primary cover plates, usually with a series of very much smaller secondary cover plates inserted distally, whereas in *Walcottidiscus* cover plates are arranged in a complex multiserial sheet, as in *Stromatocystites.*

<div align="center">

Walcottidiscus typicalis Bassler, 1935

Plate 89, figs. 2–6; text-fig. 17

</div>

    1935 *Walcottidiscus typicalis* Bassler, p. 3, pl. 1, fig. 1.
    1936 *Walcottidiscus magister* Bassler; Bassler, p. 2, pl. 2, fig. 2.
    1943 *Walcottidiscus typicalis* Bassler; Bassler and Moody, p. 210.
    1943 *Walcottidiscus magister* Bassler; Bassler and Moody, p. 210.
    1966 *Walcottidiscus typicalis* Bassler; Regnéll, p. U161.

Diagnosis. As for genus.

Types. Holotype, USNM 90754, part and counterpart (Pl. 89, figs. 2 and 3). Holotype of *Walcottidiscus magister*, USNM 90755 (Pl. 89, figs. 4–6).

Stratigraphical age and distribution. Middle Cambrian Burgess Shale, *Bathyuriscus–Elrathina* Zone, Burgess Pass, British Columbia, Canada.

Description. The preservation of the holotype, USNM 90754, is rather difficult to interpret as both part and counterpart show a mixture of mould and original plating. The more complete part shows the exterior of the underside and part of the interior of the upper surface. The less complete counterpart shows the external mould of the underside and the external surface of the upper side (text-fig. 17). The theca is somewhat distorted but appears to have had a rounded pentagonal outline. The maximum diameter is 15·5 mm and the minimum 12·0 mm, so the diameter in life must have been approximately 14·0 mm. The other specimen, USNM 90755, shows only the exterior of the upper surface and is damaged in places. It has an anterior–posterior diameter of 64·0 mm. Some of the calcite plating is preserved in this specimen. In both specimens the ambulacra extend subambitally and, in the holotype, the dorsal surface can be shown to be smaller than the thecal diameter. *W. typicalis* presumably had a sub-oval to flattened sub-globular shape in life.

    Ambulacra are arranged in a 2:1:2 pattern around the mouth. Over much of the upper surface the ambulacra are more or less straight, but on approaching the ambitus all five ambulacra curve sinistrally. In the smaller specimen, ambulacra B, C, and D appear on the lower surface, following a slightly oblique course to the margin. Adjacent ambulacra do not approach one another closely and their tips almost reach the edge of the dorsal plating. The ambulacra in the larger specimen are strongly flexed at the ambitus and run around the outer edge of the theca. The tip of one ambulacrum almost reaches the next ambulacrum to the left (Pl. 89, fig. 5).
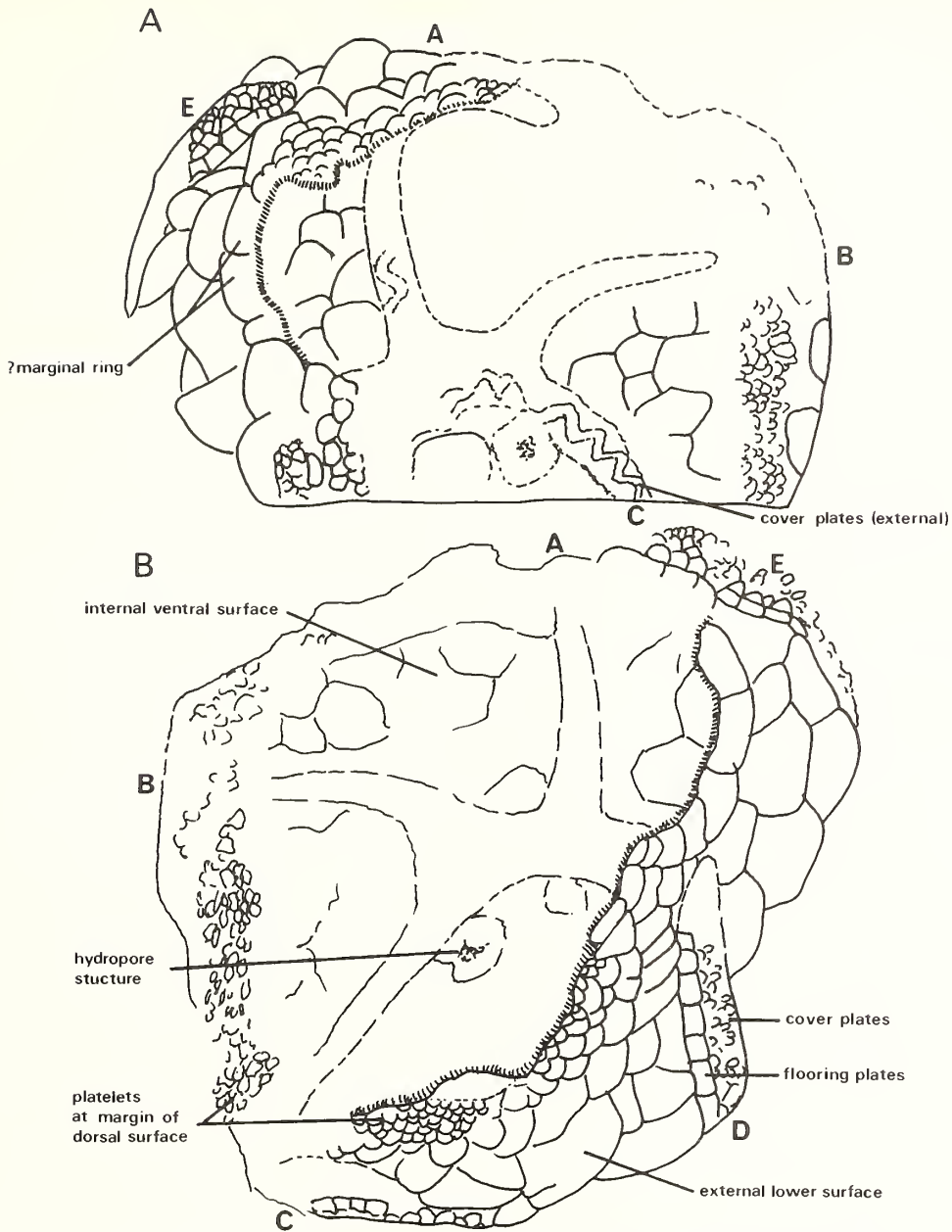
TEXT-FIG. 17. *Walcottidiscus typicalis* Bassler, 1935, USNM 90754, camera lucida drawing of the holotype: A, part; B, counterpart.

The detailed structure of the ambulacral flooring plates cannot be made out with any certainty on either specimen. Flooring plates are biserially arranged and alternate in each ambulacrum. On the outer surface the adradial portion of each flooring plate is exposed between the cover plate sheets and the interambulacral plate, as in *Stromatocystites*. This portion of the flooring plate is flat and rectangular in outline, and adjacent faces abut to form a regular border to the arch of cover plates (Pl. 89, figs. 4 and 6). The arrangement of cover plates is best

seen in the larger specimen, but can also be made out towards the tips of ambulacra B and C in the holotype. Cover plates are arranged as a multiserial sheet of abutting plates; they are largest immediately adjacent to the flooring plates and progressively decrease in size towards the free edge. Towards the distal tip in the smaller specimen, the cover plate sheet consists of just two or possibly three irregular rows, but in the larger specimen there are four or possibly five irregular rows of cover plates in each sheet. The first row of cover plates is well defined and these are the largest. They are broader than tall and more or less rectangular but with an angled upper edge making them pentagonal. There are approximately two of these primary cover plates to each flooring plate. The succeeding cover plates are much more randomly arranged and become progressively more equant in shape towards the free edge (Pl. 89, fig. 4).

The oral area is more or less totally obscured in both specimens and nothing can be seen of the oral frame. The location of the hydropore is possibly indicated by a small raised circular rim with a central depression seen on both part and counterpart of the holotype. This lies in the C/D interray, slightly removed from the oral area.

Interambulacral areas are relatively broad and are composed of large sub-polygonal and semi-tesselate plates on the upper surface, with smaller, more imbricate plates sub-ambitally. The plates imbricate adorally so that the more distal plates overlap slightly on to their more proximal neighbours. At the ambitus there are three or four plates abreast in each interambulacrum. There are no epispires.

The holotype exhibits an indistinct area of radially arranged plates in the C/D interray that may be the periproct; this lies sub-ambitally close to the edge of the ventral surface. The dorsal surface is seen only in the holotype. Much of the dorsal surface appears to have been uncalcified, since both part and counterpart reveal the inner face of the upper surface centrally. However, around the edge there is a border, 1–2 mm in breadth, composed of minute plates (3–4 per mm). The diameter of the dorsal surface is approximately 9–10 mm and so is only about 70 % of the diameter of the theca. There is a suggestion in the A/B and C/D interambulacra that the dorsal surface may be ringed by a border of broader, rather rectangular plates.

Remarks. Bassler (1935, 1936) placed these two specimens in different species. The principal differences between them are in size and degree of ambulacral curvature. Unfortunately, neither is particularly well preserved and many of the structural details are still unknown. In *W. typicalis*, although the ambulacra curve sinistrally at the ambitus, they are not particularly long and are well separated from each other. In *W. magister*, which is the larger of the two specimens, the ambulacra also curve at the ambitus to run sinistrally around the thecal margin, but in this specimen they are much longer and the tip of one ambulacrum almost touches the neighbouring ambulacrum. *W. typicalis* is only a quarter of the size of *W. magister*, so this difference could simply be a factor of growth. In all edrioasteroids with curved ambulacra, ontogenetic series show that ambulacra are initially straight in juveniles and become progressively more curved as growth proceeds. The two specimens are therefore probably no more than juvenile and adult of the same species and *W. magister* is treated as a junior synonym of *W. typicalis*.

Genus TOTIGLOBUS Bell and Sprinkle, 1978

1978   *Totiglobus* Bell and Sprinkle, p. 247.

Diagnosis. Theca sub-globular and fully plated; dorsal surface greatly reduced, less than half thecal diameter, circular in outline with marginal ring of stout plates surrounding a pavement of small polygonal plates; ambulacra more or less straight, extending sub-ambitally; flooring plates biserial, alternate, with sutural pores; cover plates in two series; oral frame composed of five compound ambulacral flooring plates; interambulacral plates imbricate to sub-tessellate, without epispires; periproct sub-ambital, close to dorsal surface.

Type species. Totiglobus nimius Bell and Sprinkle, 1978, by original designation.

Stratigraphical age and distribution. Early Middle Cambrian of Nevada, USA.

Remarks. This is probably the best understood of the Cambrian edrioasteroids because of the careful and detailed work carried out by Bell and Sprinkle (1978). *Totiglobus* can be distinguished easily from *Stromatocystites* and *Cambraster* by its interambulacral zones, which are devoid of epispires, and by its relatively small dorsal surface and swollen ventral surface; it lacks a peripheral skirt of plates, unlike *Edriodiscus. Totiglobus* most closely resembles *Walcottidiscus*, but is distinguished by having

more or less straight ambulacra at all sizes and a fully plated dorsal surface. Ambulacra in *Walcottidiscus* curve distally around the ambitus in larger individuals, and the central part of the dorsal surface is uncalcified.

Totiglobus nimius Bell and Sprinkle, 1978

1978   *Totiglobus nimius* Bell and Sprinkle, p. 247, pls. 1–6; text-figs. 1–4.

Diagnosis. As for genus.

Types. Holotype, MCZ 983; paratypes, MCZ 984–996 and NYSM 13293–13326.

Stratigraphical age and distribution. Chisholm Shale, *Glossopleura* Zone, Middle Cambrian of Nevada, USA.

Description. A full and detailed description of this species, together with full locality data, was given by Bell and Sprinkle (1978).

Genus CAMBRASTER Cabibel, Termier and Termier, 1958

1894   *Trochocystites* Miquel [*non* Barrande], p. 9.
1905   *Stromatocystites* Miquel [*non* Pompeckj], p. 476.
1923   *Cambraster* Jaekel, p. 344 [*nomen nudum*].
1935   *Cambraster* Jaekel; Stubblefield and Spencer *in* Thoral, p. 35 [*nomen nudum*].
1958   *Cambraster* Jaekel; Cabibel, Termier and Termier, p. 284.
1958   *Eikosacystis* Cabibel, Termier and Termier, p. 286.
1966   *Stromatocystites* Pompeckj; Regnéll [*pars*], p. U160.
1969   *Cambraster* (Jaekel) *emend.* Cabibel, Termier and Termier; Termier and Termier, p. 137.
1969   *Eikosacystis* Cabibel, Termier and Termier; Termier and Termier, p. 141.
1971   *Cambraster* Cabibel, Termier and Termier; Ubaghs, p. 182.

Diagnosis. Fully plated, disc shaped edrioasteroid with a pentagonal frame of stout marginal ossicles; ambulacra straight, inserted distally between the marginal ossicles; dorsal surface plated, slightly larger than ventral surface, and composed of a sub-tesselate pavement of plates arranged in cycles; interambulacral zones with epispires.

Type species. Cambraster cannati (Miquel, 1894), by original designation.

Other species. C. tastudorum Jell, Burrett and Banks, 1985.

Stratigraphical age and distribution. Paradoxides mediterraneus Zone, Middle Cambrian of the Montagne Noire, southern France; medial Middle Cambrian of Tasmania.

Remarks. This important genus remained poorly understood until Ubaghs (1971) published a detailed morphological description of well-preserved material. The name *Cambraster* was first used by Jaekel (1923) for a species that he believed to be a primitive asteroid from the Middle Cambrian sandy schists of the departement of Hérault, France. He interpreted *Cambraster* as intermediate between edrioasteroids and the Ordovician asteroid *Archegonaster*, but failed to describe or figure this animal, or even to designate a specific name. Prior to this, specimens of *Cambraster* had been wrongly identified as the carpoid *Trochocystites* or as *Stromatocystites* by Miquel (1894, 1905). Although later authors have been uncertain as to the identity of Jaekel's *Cambraster*, Stubblefield and Spencer (*in* Thoral 1935) suggested that it was the same as Miquel's (1905) species *S. cannati*, also from the Middle Cambrian of Hérault. Amongst the papers in the possession of W. K. Spencer at his death, and now in the archives of the British Museum (Natural History), is an original line-drawing signed by Jaekel and labelled *Cambraster* (text-fig. 18), proving that Jaekel was indeed referring to the same animal as Miquel.

The name *Cambraster* was finally validated by Cabibel, Termier and Termier (1958) who provided a generic diagnosis and gave a rather sketchy description of the type species, *C. cannati* (Miquel); they also described a new genus *Eikosacystis*, with two species. These were all redescribed in slightly greater detail by Termier and Termier (1969) who placed *Cambraster* and *Eikosacystis* in their own
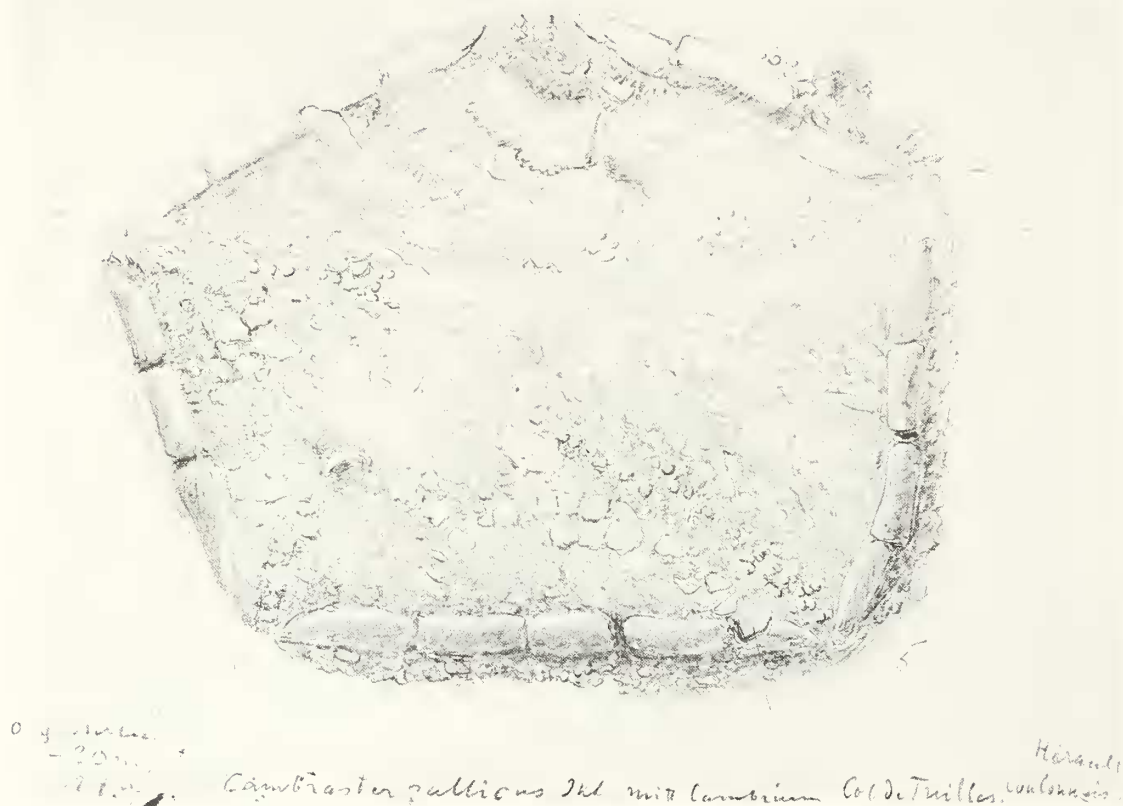
TEXT-FIG. 18. Original line drawing by Otto Jaekel of a specimen said to be in the Berlin Museum and signed as *Cambraster gallicus* Jkl, Middle Cambrian, Coulounnais, Hérault.

families, the Cambrasteridae and the Eikosacystidae respectively. However, as Ubaghs (1971) pointed out, *Cambraster* and *Eikosacystis* are synonymous and differ only in their state of preservation. Specimens with the plating of the oral surface preserved more or less intact, and therefore showing ambulacra, were placed by the Termiers into *Cambraster* while more distorted specimens that had either a jumbled muddle of dissociated plates within the marginal ring or had lost the ventral plating altogether (and so revealed the interior of the dorsal surface) were classified as *Eikosacystis*, which was thus believed to lack ambulacra. Ubaghs's (1971) careful and detailed observations on *Cambraster* have greatly clarified the status of this genus while further morphological information has been added by the discovery of additional material from the Cambrian of Tasmania by Jell *et al.* (1985).

  Cambraster is easily distinguished from other Cambrian edrioasteroids by its prominent marginal ring of ossicles which, unlike those of *Edriodiscus*, are not inserted into the dorsal pavement.

Cambraster cannati (Miquel, 1894)

Text-figs. 2, 3, 6A, 18, 19

1894   *Trochocystites cannati* Miquel, p. 9.
1905   *Trochocystites* sp. Miquel, p. 475.
1905   *Stromatocystites cannati* (Miquel); Miquel, pp. 476, 482, pl. 15, fig. 5.

1935   *Stromatocystites*(?) *Cannati* Miquel; Thoral, p. 35.
1935   *Trochocystites*(?) *nov. sp.* Miquel; Thoral, p. 138, pl. 5, fig. 3.
1958   *Cambraster cannati* (Miquel); Cabibel, Termier and Termier, p. 284, pl. 1, figs. 2–4; text-
        figs. 3 and 4.
1958   *Eikosacystis couloumanensis* Cabibel, Termier and Termier, p. 286, pl. 1, fig. 5; text-fig. 5.
1958   *Eikosacystis? ferralsensis* Cabibel, Termier and Termier, p. 287, pl. 1, figs. 6 and 7.
1969   *Cambraster cannati* (Miquel); Termier and Termier, p. 138, pl. 9, figs. 1–3; text-fig. 5.
1969   *Cambraster elegans* Termier and Termier, p. 139, pl. 10, figs. 1–4; text-fig. 6.
1969   *Eikosacystis couloumanensis* Cabibel, Termier and Termier; Termier and Termier, p. 141, pl. 12,
        fig. 1; text-fig. 7.
1969   *Eikosacystis miqueli* Termier and Termier, p. 142, pl. 11, figs. 1–4; text-fig. 8.
1969   *Eikosacystis courtessolei* Termier and Termier, p. 143, pl. 12, fig. 2; text-fig. 9.
1969   *Eikosacystis ferralsensis* Cabibel, Termier and Termier; Termier and Termier, p. 144, pl. 12, figs. 3
        and 4; text-fig. 10.
1971   *Cambraster elegans* Termier and Termier; Ubaghs, p. 182, text-figs. 8–11.

Diagnosis. As for genus.

Types. The holotype of *Cambraster cannati*, *C. elegans*, and *Eikosacystis miqueli* are currently held at the Museum of Le Havre, France. Latex casts (BM(NH) E63135, 63136, and 63153) of these specimens were studied (text-fig. 19). The whereabouts of *E. ferralsensis*, *E. couloumanensis*, and *E. courtessolei* are currently unknown. They were in the possession of Mme G. Termier at the Département de Géotectonique, Université Pierre et Marie Curie, Paris, but, on enquiry there, could not be located.

Stratigraphical age and distribution. All the material comes from Beds E and F of Courtessole (1973) in the Middle Cambrian of the Montagne Noire, in the vicinity of Coulouma and Ferrals-les-Montagnes, France.

Description. A complete and detailed description of this species was given by Ubaghs (1971), under the name *C. elegans*, and I have only two additional observations to make. First, although dorsal plating is generally disrupted to a greater or lesser degree in all of the specimens examined, plates do have an angular outline and would have formed a continuous pavement of closely fitting plates in life, as in *Stromatocystites*. These plates are arranged in circles around the centre of the disc with at least two rings of larger plates separated by zones of smaller plates. Secondly, the peripheral zone of dorsal plating does not extend much beyond the ring of marginal ossicles and only a very narrow rim of dorsal plates would have been visible from above.

Remarks. Termier and Termier (1969) recognized two species of *Cambraster* and four of *Eikosacystis*, all of which are treated here as synonymous. Two of their species, *C. cannati* and *C. elegans*, are moderately well preserved and show the plating of the oral surface. These two species were distinguished by the fact that in *C. elegans* rather more of the dorsal surface plating is visible around the margin. This is a post-mortem artifact produced by displacement of some of the marginal ring ossicles and, as the two specimens are otherwise identical, I regard them as synonymous. Two of the Termier's species which show only the marginal ring and dorsal plating, *E. miqueli* and *E. courtessolei*, are indistinguishable from one another. Furthermore, as Ubaghs (1971) pointed out, *E. miqueli* and *C. elegans* are specimens of the same species in different states of preservation, one showing the marginal ring and aboral surface, the other showing the marginal ring and oral surface. Specimens referred to as *E. ferralsensis* are large distorted individuals in which most of the plating within the marginal ring lies jumbled together or has been lost. Finally, *E. couloumanensis* is known from only a single small specimen, 12 mm in diameter. This has a stout marginal ring of equant ossicles but the plating within the marginal ring is poorly preserved. I have not been able to examine this specimen but, as it comes from the same beds and the same locality as adult *C. cannati*, I suspect that it is a juvenile specimen of this species.

Cambraster tastudorum Jell, Burrett and Banks, 1985

Remarks. This species has only recently been described by Jell *et al.* (1985) from the Cateena Group, medial Middle Cambrian, of Tasmania. It differs from *Cambraster cannati* in having epispires
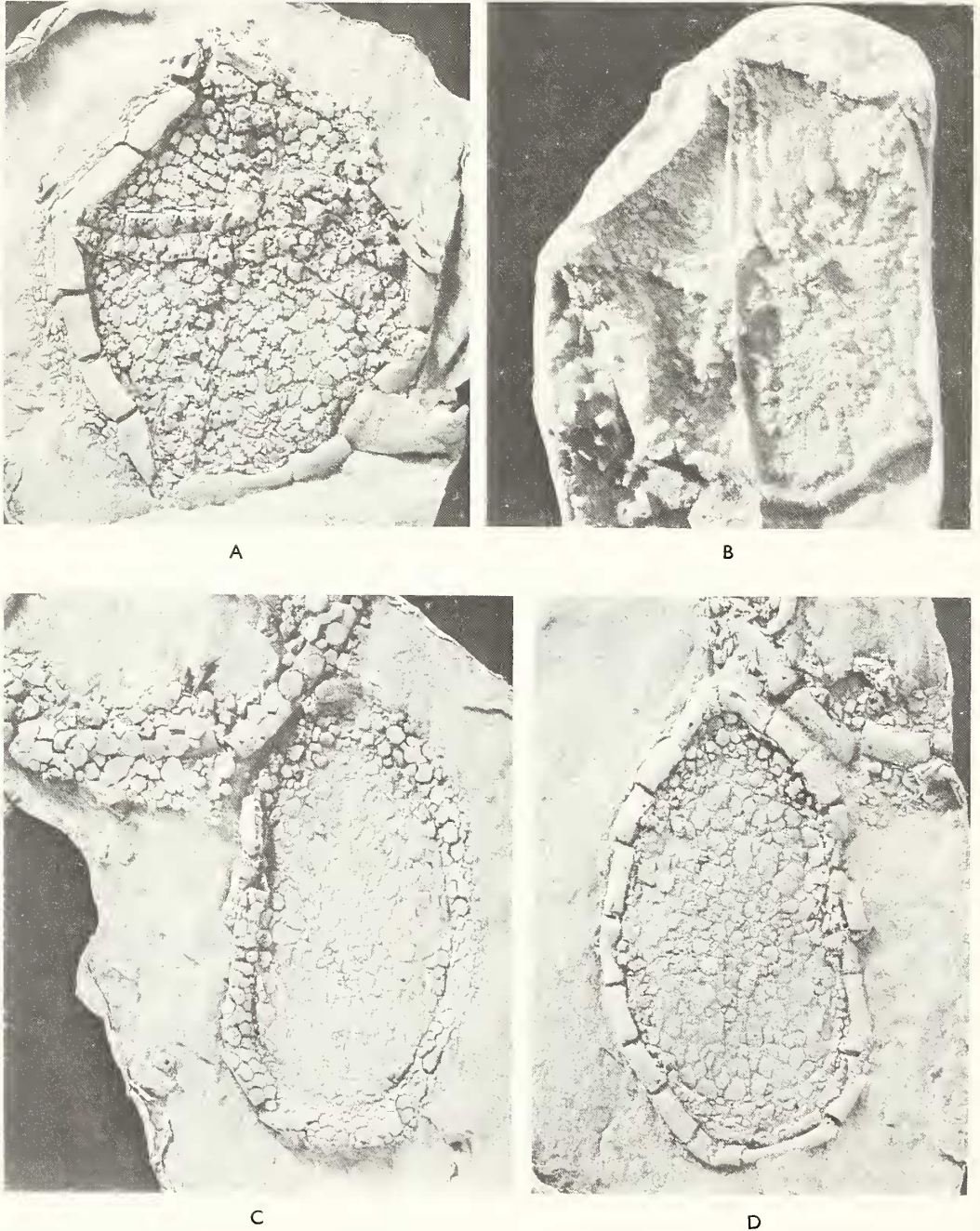
TEXT-FIG. 19. *Cambraster cannati* (Miquel, 1894). A, BM(NH) E63135, latex cast of the holotype of *C. elegans* Termier and Termier, 1969, ventral surface, ×3 (see text-fig. 2). B, BM(NH) E63153, latex cast of the holotype of *Trochocystites cannati* Miquel, 1894, ×1·4. C, D, BM(NH) E63136, latex casts of the holotype of *Eikosacystis miqueli* Termier and Termier, 1969 (see text-fig. 3): C, aboral surface, exterior, ×3; D, counterpart showing the ventral surface of the marginal ring and the interior of the dorsal surface (all ventral disc plating having been lost), ×3.

developed only towards the centre of the oral surface and in having a prominent contiguous circle of large polygonal plates near the centre of the aboral surface.

Genus EDRIODISCUS Jell, Burrett and Banks, 1985

1971   *Cyclocystoides* Henderson and Shergold [*non* Salter and Billings], p. 706.
1985   *Edriodiscus* Jell, Burrett and Banks, p. 190.

Diagnosis. Aboral surface fully plated, composed of small polygonal plates with radial ridging; marginal ring circular, composed of forty to fifty plates, surrounded by a peripheral skirt; ventral surface unknown.

Type species. Cyclocystoides primotica Henderson and Shergold, 1971, by original designation.

Stratigraphical age and distribution. Early Middle Cambrian of West Queensland, Australia.

Remarks. This genus is very poorly known and contains just one species represented by two specimens, neither of which reveals the ventral surface. It is, however, distinct from any other known echinoderm and clearly deserves generic separation. The species was originally placed in the genus *Cyclocystoides* by Henderson and Shergold (1971), but Smith and Paul (1982) pointed out that it lacked important cyclocystoid features such as perforate marginal ossicles, and removed it from that group.

Edriodiscus, with its stout marginal ring of abutting ossicles, most closely resembles *Cambraster*. However, there are only fifteen to twenty marginal ossicles in *Cambraster*, and these are hidden from view on the lower surface by the pavement of dorsal plates. Marginal ossicles in *Edriodiscus* are more numerous and are inserted into the dorsal pavement. No other Cambrian echinoderm has a peripheral skirt of plates so well developed. The radial ridges that are such a prominent feature of this animal are highly reminiscent of the radial ridging present on the lower surface of peripheral plates of agelacrinitids, and presumably served the same adhesive function. Nothing is known about the oral surface.

Edriodiscus primotica (Henderson and Shergold, 1971)

Text-fig. 20

1971   *Cyclocystoides primotica* Henderson and Shergold, p. 706, pl. 138, figs. 1–3.
1985   *Edriodiscus primotica* (Henderson and Shergold); Jell, Burrett and Banks, p. 190, figs. 7a–c and 8.
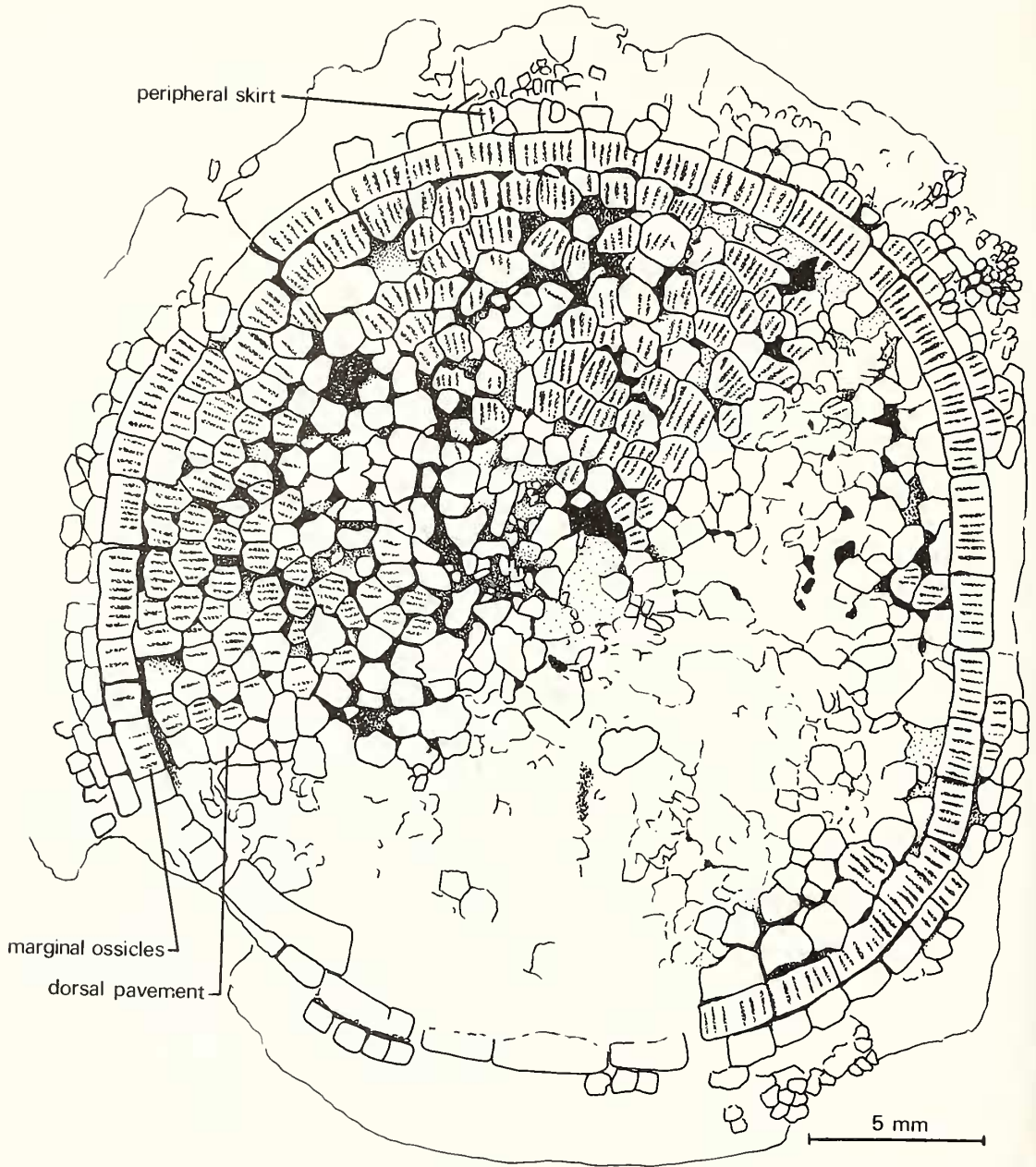
Diagnosis. As for genus.

Types. Holotype, CPC 11395 (text-fig. 20); paratype, CPC 11396.

Stratigraphical age and distribution. Yelvertoft Beds, late Ordian, early Middle Cambrian of West Queensland, Australia.

Description. A full description of the lower surface of this species was given by Henderson and Shergold (1971) and I have nothing new to add. New material, showing details of the ventral surface, has recently been found by Peter Jell and a more complete description has been given by him (Jell *et al.* 1985).

peripheral skirt

marginal ossicles

dorsal pavement

5 mm

TEXT-FIG. 20. *Edriodiscus primoticus* (Henderson and Shergold, 1971), CPC 11395, camera lucida drawing of the holotype, dorsal surface.

REFERENCES

BASSLER, R. S. 1935. The classification of the Edrioasteroidea. *Smithson. misc. Collns*, **93**, 1–11.
—— 1936. New species of American Edrioasteroidea. Ibid. **95**, 1–33.
—— and MOODY, M. W. 1943. Bibliographic and faunal index of Palaeozoic pelmatozoan echinoderms. *Spec. Pap. geol. Soc. Am.* **45**, 733 pp.
BATHER, F. A. 1899. A phylogenetic classification of the Pelmatozoa. *Rep. Br. Ass. Advmt Sci.*, D, 916–923.
—— 1900. The Echinoderma. *In* LANKESTER, E. R. (ed.). *A Treatise on Zoology*, part 3, 216 pp. Black, London.
—— 1915. *Studies in Edrioasteroidea 1–IX*, 403 pp. Published by the author at 'Fabo', Marryat Road, Wimbledon, England.
BELL, B. M. 1976. A study of North American Edrioasteroidea. *Mem. N.Y. St. Mus. Sci. Serv.* **21**, 447 pp.
—— 1977. Respiratory schemes in the Class Edrioasteroidea. *J. Paleont.* **51**, 619–632.
—— 1980. Edrioasteroidea and Edrioblastoidea. *In* BROADHEAD, T. W. and WATERS, J. A. (eds.). Echinoderms, notes for a short course. *Univ. Tennessee, Dept. geol. Sci. Stud. Geol.* **3**, 158–174.
—— and SPRINKLE, J. 1978. *Totiglobus*, an unusual new edrioasteroid from the Middle Cambrian of Nevada. *J. Paleont.* **52**, 243–266.
BOCKELIE, F. and PAUL, C. R. C. 1983. *Cyathotheca suecica* and its bearing on the evolution of the Edrioasteroidea. *Lethaia*, **16**, 257–264.
CABIBEL, J., TERMIER, H. and TERMIER, G. 1958. Les Échinoderms mésocambriens de la Montagne Noire. *Annls Paléont.* **44**, 281–294.
CHAPMAN, E. J. 1860. On a new species of *Agelacrinites* and on the structural relations of that genus. *Can. J. Ind. Sci. & Art*, **5**, 358–365.
COURTESSOLE, R. 1973. Le Cambrien Moyen de la Montagne Noire: biostratigraphie. Laboratoiro de Geologie CEARN, Toulouse.
FELL, H. B. 1962. A classification of the echinoderms. *Tuatara*, **10**, 138–140.
—— 1963. Phylogeny of sea-stars. *Phil. Trans. R. Soc.* **B246**, 381–435.
—— 1965. The early evolution of the Echinozoa. *Breviora*, **219**, 1–17.
HENDERSON, R. A. and SHERGOLD, J. H. 1971. *Cyclocystoides* from the early Middle Cambrian rocks of north-western Queensland, Australia. *Palaeontology*, **14**, 704–710.
HOLLOWAY, D. J. and JELL, P. A. 1984. Silurian and Devonian edrioasteroids from Australia. *J. Paleont.* **57**, 1001–1016.
JAEKEL, O. 1899. *Stammesgeschichte der Pelmatozoen, 1: Thecoidea und Cystoidea*, 442 pp. Berlin.
—— 1918. Phylogenie und System der Pelmatozoen. *Paläont. Z.* **3**, 1–128.
—— 1923. Zur Morphologie der Asterozoa. Ibid. **5**, 344–350.
JELL, P. A., BURRETT, C. F. and BANKS, M. R. 1985. Some Cambrian and Ordovician echinoderms from eastern Australia. *Alcheringa*, **9**, 183–208.
KESLING, R. V. 1967. Edrioasteroid with unique shape from Mississippian strata of Alberta. *J. Paleont.* **41**, 197–202.
MIQUEL, J. 1894. Note sur la géologie des terrains primaires du département de l'Hérault. Le Cambrien et l'Arenig. *Bull. Soc. Étude Sci. nat. Béziers*, **17**, 5–36.
—— 1905. Essai sur le Cambrien de la Montagne Noire. Coulouma, l'Acadien. *Bull. Soc. géol. Fr.* (4), **5**, 465–483.
PAUL, C. R. C. and SMITH, A. B. 1984. The early radiation and phylogeny of echinoderms. *Biol. Rev.* **59**, 443–481.
POMPECKJ, J. F. 1896. Die Fauna des Cambrium von Tejrovic und Skrej in Bohmen. *Jb K.-K. geol. Reichsanst.*, Wien, **45**, 495–614.
REGNÉLL, G. 1945. Non-crinoid Pelmatozoa from the Palaeozoic of Sweden, a taxonomic study. *Meddn. Lunds geol.-min. Instn*, **108**, 255 pp.
—— 1966. Edrioasteroids, pp. U136–U172. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part U. Echinodermata 3*. Geological Society of America and University of Kansas Press, New York and Lawrence, Kansas.
SCHUCHERT, C. 1919. A Lower Cambrian edrioasteroid *Stromatocystites walcotti*. *Smithson. misc. Collns*, **70**, 1–7.
SMITH, A. B. 1984a. *Echinoid palaeobiology*, 190 pp. George Allen & Unwin, London.
—— 1984b. Classification of the Echinodermata. *Palaeontology*, **27**, 431–459.
—— and PAUL, C. R. C. 1982. A revision of the class Cyclocystoidea (Echinodermata). *Phil. Trans. R. Soc.*, **B296**, 577–684.
TERMIER, H. and TERMIER, G. 1969. Les Stromatocystitoides ct leur descendance: essai sur l'evolution dcs premiers echinoderms. *Geobios*, **2**, 131–156.

TERMIER, H. and TERMIER, G. 1980. Modalités de l'évolution des Echinodermes au Cambrien. *In* JANGOUX, M. (ed.). Echinoderms: present and past, 59–65. A. A. Balkema, Rotterdam.

THORAL, M. 1935. *Contribution a l'étude paleontologique de l'Ordovicien intérieur de la Montagne Noire et révision sommaire de la fauna cambrienne de la Montagne Noire*, 362 pp. Imprimerie de la Manufacture de la Charité, Montpellier.

UBAGHS, G. 1971. Diversité et specialisation des plus anciens echinodermes que l'on connaisse. *Biol. Rev.* **46,** 157–200.

WILEY, E. O. 1979. An annotated Linnaean hierarchy, with comments on natural taxa and competing systems. *Syst. Zool.* **28,** 308–337.

ZELIZKO, J. C. 1911. Nove prispevky ke studiu jineckeho kambria. *Rozpr. česke Akad.* **20** (10), 1–7.

ANDREW B. SMITH

Department of Palaeontology
British Museum (Natural History)
Cromwell Road
London SW7 5BD